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Is fracture a bigger problem for smaller animals? Force and fracture scaling for a simple model of cutting, puncture and crushing

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Many of the materials that are challenging for large animals to cut or puncture are also cut and punctured by much smaller organisms that are limited to much smaller forces. Small organisms can overcome their force limitations by using sharper tools, but one drawback may be an increased susceptibility to fracture. We use simple contact mechanics models to estimate how much smaller the diameter of the tips or edges of tools such as teeth, claws and cutting blades must be in smaller organisms in order for them to puncture or cut the same materials as larger organisms. In order to produce the same maximum stress when maximum force scales as the square of body length, the diameter of the tool region that is in contact with the target material must scale isometrically for punch-like tools (e.g. scorpion stings) on thick targets, and for crushing tools (e.g. molars). For punch-like tools on thin targets, and for cutting blades on thick targets, the tip or edge diameters must be even smaller than expected from isometry in smaller animals. The diameters of a small sample of unworn punch-like tools from a large range of animal sizes are consistent with the model, scaling isometrically or more steeply (positively allometric). In addition, we find that the force required to puncture a thin target using real biological tools scales linearly with tip diameter, as predicted by the model. We argue that, for smaller tools, the minimum energy to fracture the tool will be a greater fraction of the minimum energy required to puncture the target, making fracture more likely. Finally, energy stored in tool bending, relative to the energy to fracture the tool, increases rapidly with the aspect ratio (length/width), and we expect that smaller organisms often have to employ higher aspect ratio tools in order to puncture or cut to the required depth with available force. The extra stored energy in higher aspect ratio tools is likely to increase the probability of fracture. We discuss some of the implications of the suggested scaling rules and possible adaptations to compensate for fracture sensitivity in smaller organisms.

1. Introduction

A mosquito and a wolf must both puncture the same elk skin, yet a mosquito can only apply about $1/10^5$ of the force that a wolf can apply and is only roughly $1/10^8$ as powerful as the wolf. Leaf cutter ants, snails and howler monkeys puncture and cut the same leaves; large and small animals consume the same hard seeds. One way that smaller organisms can overcome force limitations is with sharper tools.

In our modelling, sharpness is a property of the cutting or puncturing interaction rather than of the blade or punch: 'sharper' indicates here that a smaller area of the tool is in contact with the target when fracture of the target begins,

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with the size of the contact region quantified here by its effective diameter in the plane perpendicular to the penetration force. By defining sharpness in terms of contact area, the natural scale in contact mechanics, the results here are generalizable to cases where the tool deforms as it punctures or cuts, increasing the contact region, and to cases where the target is soft and deforms around the smallest diameter part of the tip without damage.

We have previously argued that if smaller organisms are subjected to nearly the same forces or impacts as larger organisms, then fracture resistance may be of critical importance because of the smaller cross-sectional areas of the smaller organism's mechanical structures [1]. For this reason, smaller organisms might be more likely to trade other desirable mechanical properties, like hardness, for greater fracture resistance.

In addition, smaller organisms produce smaller forces and must have smaller contact areas for their claw tips, teeth, stings, etc., in order to produce pressure (force per unit area) that is equal to the maximum pressure produced by larger organisms. The sharper structures (edges or points) would probably be more susceptible to damage from fracture, because less energy is required to fracture lower cross-section regions into pieces.

Here we detail and begin testing the hypothesis that fracture is a bigger problem in smaller animals. First, we discuss how the force required to puncture or cut scales with sharpness, and then we attempt to predict how likely tools subjected to these force levels are to fracture catastrophically in puncture and cutting attempts. We quantify the scaling relations between sharpness and required force using contact mechanics for models of punch-like tools, such as teeth, and for cutting blades. Our approach is to use the homogeneous linear elastic models and other simplifications commonly used in contact mechanics. Because real biological materials are not as simple as these models [2], we test predictions of force versus diameter scaling using a size range of actual biological tools.

We attempt to predict the likelihood of tool fracture by hypothesizing that the likelihood of fracture increases with an increase in the ratio of the minimum energy required to fracture the tool in two, to the maximum energy stored in deformation of the tool and target during the penetration process. In particular, we hypothesize that, for a wide range of cases, the energy to fracture the tool is proportional to the square of the tool diameter, whereas the energy to puncture the target typically increases linearly as the tool diameter.

Puncture and cutting involve fracture, elastic stretching and viscoelasticity. However, cutting and puncture of most natural food sources is dominated by fracture [2–4]. Fracture is the process of breaking the bonds that hold two surfaces together [3]. Fracture requires a minimum total energy given by the sum of the energies required to break each of the individual bonds (here we use bonds in the general sense of a force keeping the material together, including friction forces). Initiation of fracture is predicted by several similar theories of failure; we use the maximum shear stress theory, which suggests that fracture begins when the maximum shear stress exceeds a threshold. However, the results would be the same for maximum principal stress and other theories.

We assume that small and large animals have to apply enough force to exceed a stress threshold in the target under their cutting and puncturing tools, in order to initiate the cut or puncture. With this assumption, the relationship between sharpness and force is clear. Sharper tools have lower contact area and thus produce higher pressures and stresses for the same force on the tool.

Once the organism has fractured the fracture-resistant surface membrane of the target plant or animal, using its cutting and puncturing tools, a weaker internal material is sometimes fractured by molar-like tools [5] that fracture the material into smaller pieces, improving digestion efficiency by increasing the exposed surface area [2,4,6]. This fracture by 'crushing' between two molar-like surfaces also requires that a certain stress level be exceeded, and so the 'molar' area of smaller organisms would be expected to decrease with body size if the organisms are force-limited. However, we suggest that even large grazing animals are likely to be approximately force-limited for energy reasons. The optimal strategy for maximizing the rate of energy intake of low energy-density materials like leaves [5], is, we argue, the strategy of setting the total crushing area, so that the maximum jaw muscle forces produce stresses that just meet the threshold needed to initiate the fractures that break apart the target material. By having the maximum possible crushing area, the animal maximizes the potential food energy intake rate. Thus, we argue that the crushing area is given by maximum force for a large range of animal sizes.

Fracture scaling relations have been developed to explain scaling of bone sizes with body size. Scaling of bone length and diameter is consistent with a simple model in which the bones are considered to be cylinders, and it is assumed that the bones are sized so that bending and compressive stresses are independent of body size [7,8]. Here we develop similar models for scaling fracture in tools and their targets.

We argue that the mechanical, material and behavioural adaptations that small animals employ to overcome force limitations are integral to their ecology and evolution; circumventing force limitations allows new energy sources and new niches to become available to small animals.

2. Experimental

2.1. Force and energy to puncture versus tool diameter

Both pristine and worn tools were selected for puncture measurements. Specimens and their sources are summarized in the data tables in the results section. We selected tools that had steep (less than about 20 degrees from the long axis) sides, so that the tool would be in contact with the target only at the tip. By observing the puncture process, we were able to make sure that this was the case and the tip diameter was the appropriate contact diameter. The tools were dissected free and attached with epoxy at the tip of a glass triangle, cut from a microscope slide, that attached to the test instrument.

The test instrument was originally built to measure the energy of fracture of small specimens [1] and was modified to hold the tool specimen assembly and the target materials on the load cell and translation stage, respectively. The target assembly was moved towards the tool by a powered micrometer. Both the force measured by the load cell and the extension of the powered micrometer were recorded by a computer and force–displacement curves were generated. Energy was measured by integrating under the force–displacement curves. Averages of three runs were used to reduce statistical fluctuations.

We measured the force and energy required to puncture targets that were either thin or thick on the scale of the tool

tip diameters. For the thin target, we used 0.038 mm Cellophane (chosen because it is an isotropic membrane of cellulose chains and thus somewhat similar to the cellulose in plants and the chitin in insects), adhered over an aluminium frame with a 5 mm hole in it. The tool and target were aligned, so that the Cellophane would be punctured at the centre of the 5 mm diameter unsupported region.

For the thick target, we used a 2 cm thick (much greater than the maximum tool penetration) sample of acrylic polymer emulsion (Golden GAC-200). We checked that we had correctly identified the point in the force displacement curve at which a crack first began using multiple preliminary tests with different maximum forces. In general, there was a large drop in required force when the surface was first penetrated with a crack. During these preliminary tests, any cracks were made visible in the transparent material by applying ink from a Sharpie marker after an attempted penetration. Capillary forces drew the ink into the cracks.

2.2. Sharpness versus body length data for pristine tools

Two types of tools were selected for comparing tip diameter with body length. The first included tools used primarily for cutting and puncturing of food material. These included the incisors of mammals, the largest tyne (prong) of the cheliceral finger of a scorpion, and a marginal tooth from a spider. The second tool type consisted of the leg claws, mainly from the same organisms. The leg claws that we used were conical, reaching a small point, rather than, for example, adhesive pads. They may be used to help penetrate prey or to penetrate a substrate, like bark, to improve grip. Specimen details are in the data tables.

To avoid the potential masking effects of wear, which have been thought to hide scaling relationships in vertebrate teeth [9], we used pristine tools, obtained either just before or after moulting or birth.

Animals were selected mainly on the basis of commercial availability of breeding animals or animals with pristine tools, or our ability to collect and raise individuals from the wild. Specimens and sources are summarized along with the data in tables in the results section.

Tool tips and edges were first examined using a Zeiss STEMI SV8 dissecting microscope, and, if large enough to image optically, photographed together with an appropriate scale using a Sony DSC-R100M2 camera, custom installed on the microscope. For tools with radii too small to image optically, a scanning electron microscope was used to examine uncoated specimens.

The tips of punch-like tools were imaged with the long axis of the tool in the plane of the image, so that the tip could be visually fitted with a line or circle. Blades were imaged, so that a cross section was in silhouette (e.g. if the blade did not follow a straight line, then the cross section could be imaged at the extreme of a protruding portion). We assumed that the tips of the tools were cylindrical and measured the diameter from only one angle. Imperfect diameter estimation owing to variations from cylindrical symmetry at the tip would have a small effect when plotting tip size over several orders of magnitude.

The diameter of a circle fitting the projection of the tip in the microscope or SEM image was measured using 'IMAGEJ'

analysis software (National Institutes of Health, http://rsbweb.nih.gov/ij/index.html). For plots of tool diameter versus body length, we used the length of the source individual (rather than a species average).

2.3. Aspect ratio measurement

The aspect ratio of a tool was taken to be the ratio of tool length to the minimum width at the midpoint of the length. The length was taken to be the distance from the tip to the first abrupt increase in diameter of the tool. Thus, for mammals, the length of a tooth was taken to be the distance from the tip to the gum line. We use this definition, because we are interested in energy storage during deflection, which, for beams, decreases as the fourth power of the diameter in homogeneous materials. Because energy storage during beam deflection is so strongly dependent on diameter, most of the energy is likely to be stored distal to any abrupt increase in diameter. The width was taken to be the minimum midpoint width if the cross section was not circular, because smaller widths dominate energy storage. This differs slightly from previously used measurements [10].

3. Hypotheses and initial tests

3.1. Smaller organisms need sharper tools to overcome force limitations; in our model, puncturing tool tips scale with an exponent ≥ 1, and cutting blades ≥ 2

3.1.1. The forces required to produce the same stress under puncturing or cutting tools that differ only by tip or edge diameter

Immediately prior to puncture, the target material is indented by the tool, to produce stresses that may initiate fracture and penetration. Material failure is predicted, by maximum shear stress theory, to begin when the shear stress exceeds a threshold. On this basis, we assume that the animal must reach a threshold stress beneath its sting or tooth in order to initiate the fractures that allow penetration of the target. One related assumption that we make is that the density of any fracture-initiating defects [11,12] is great enough that there is a high probability that defects exist in the high-stress region under the smallest tool. The distribution of stresses beneath the indenter are given by contact mechanics, but the scaling relationships can be obtained simply from symmetry or dimensional analysis. There are two limiting cases; in the first, the target membrane is thick compared with the diameter of the tool at the border of the contact region between tool and target; for this case, the target is modelled as an elastic half-space. In the second limiting case, the target membrane is thin compared with the diameter of the contact region. We also consider two types of tools: punches and cutting blades. For punches, such as stings, canine teeth and claws, the contact area increases in two dimensions as the diameter of the tool increases. For the purpose of our model, we define cutting blades as tools whose contact with the target only increases in one dimension as the tool diameter increases; cutting is initiated over a region smaller than the length of the blade, so increasing the diameter of

the blade edge increases the contact area, but increasing the length of the blade does not.

Thick target

Punch. For the punch, modelled as a sphere pressing into an elastic half-space, any of the stresses in the target are proportional to the maximum pressure, so the relationship between stress (S), the force pressing the tool into the target (F) and the diameter of the circular cross section of the sphere where it is in contact with the target (D) is $S \propto F/D^2$ [13, pp. 93–94]. Thus, the force on the punch must increase with the square of the diameter of this contact zone in order to obtain the same stress beneath it, $F_{\text{punch-thick}} \propto D^2$.

Cutting blade. For the cutting blade, modelled as an infinitely long cylinder parallel to and pressing into the surface of an elastic half-space, the stress relationship is $S \propto F/D$, where F is the applied force and D is the diameter or width of the contact region [13, pp. 101–102]. Thus, the applied force must increase linearly with the diameter of the blade edge in order to produce the same stress beneath the blade, $F_{\text{blade-thick}} \propto D$.

Thin target

Punch. Predictions using the Hertzian half-space conditions are essentially correct up until the point where the thickness of the membrane is about two times the diameter of the contact region. As the ratio of contact region diameter to target thickness increases, the transition to a thin plate condition occurs, with most of the transition between when the contact region diameter is about equal to the membrane thickness and when the contact region is twice the membrane thickness [14, p. 686]. The location of maximum stress moves from under the centre of the punch, out to its edges, as the membrane bends, and the stresses are mainly owing to bending stresses [14, p. 686] and [13, p. 143]. Because the pressure is high only at the perimeter of the area of contact, and the width of this high-pressure region does not increase with tool size, the area of the region of high pressure increases only with the diameter of the contact region, not with the square of the diameter as it does for the thick target. The force on the punch must increase only as the diameter in order to maintain the same pressure over this increased area, $F_{\text{punch-thin}} \propto D$.

Cutting blade. For the cutting blade on a thin target, the pressure is nearly all at the edge of the contact region, as with the punch. But because the length, and thus the area, of the edge region does not increase with force or edge diameter, the required force no longer increases with the blade edge diameter and is constant, $F_{\text{blade-thin}} = C$. A likely response for the force-limited organism would be to reduce the contact area between the blade and the target or to use other force reduction techniques such as slice–push cutting [3].

The results from contact mechanics accurately predict stress distributions when the deflections are small and for highly symmetric tools like the sphere and cylinder modelled above. However, the scalings with force can also be obtained using more generalizable symmetry arguments and dimensional analysis. For linear elastic interactions, there is no absolute length scale in the model, and hence if all of the spatial relationships are the same (i.e. the picture is the same, meaning that the tool and target scale isometrically), then the stresses in the target will reach the same value, independent of absolute tool size. The spatial relationships will be the same if the pressure (force per unit area) at the interface of

the target and the tool is the same and if the tools are internally isometric (all dimensions of two such tools are multiples of the same factor). The pressure will remain the same for isometric tools if the force applied to the tool is proportional to the area of the region where the pressure is not zero. This argument, that applied force must be proportional to the area of the non-zero pressure region at the tool–target interface in order to produce equal stresses, leads to the same relations as obtained above.

The quantity D, the effective diameter of the tool at the border of the region of contact (the square root of the cross-sectional area for non-cylindrical punches), thus scales with any dimension of the isometric tools when the force on the tools is enough to initiate fracture in a particular material. This diameter, D, needs to be measured in order to test that this model is predictive for real tools. However, the diameter of the tool at the edge of the contact region depends on the target material: the contact region may be larger for softer materials. To avoid this problem, we tested the model using tools that resemble a steep cone (less than 20 degrees from the long axis), so that the material would be in contact only at the end of the cylinder.

In summary, if one tip is of half the diameter of the other, the required force will be one-fourth for a punch on a thick target, half for a blade on a thick target, half for a punch on a thin target and unchanged for a blade on a thin target.

3.1.2. Experimental verification that maximum force required to puncture increases with tool diameter for a thin target and the square of diameter for a thick target

The scaling of puncture force with tool diameter from the simple model also appears to apply to more complex targets. The force to puncture pig skin with hemispherical tipped cylinders, 3–8 mm in diameter, scaled isometrically with the diameter of the cylinder [15]. Puncture tests of 0.3–1 mm thick elastomer membranes showed that the force required to puncture scaled with the diameter of the 0.1–2.5 mm cylinders, and that there was no difference in required force for flat-tipped or rounded cylinders [16]. We tested that this scaling rule also applies to punctures using different animal tools.

Figure 1 shows results from puncturing thick and thin targets with the selection of tools in table 1. The fits of the data suggest that the model does a good job predicting the scaling for this variety of tools: on the thin target, the fit is consistent with $F_{\text{punch-thin}} \propto D$, but not D^2 ($p < 0.00002$), and the fit for the thick specimen data is consistent with $F_{\text{punch-thick}} \propto D^2$, but not D ($p < 0.03$).

3.1.3. The forces required to produce the same stress under crushing tools that only differ in crushing surface area

Crushing, as between molar-like tools, is also a fracture process, initiated by high stresses. The peak stress generated in an elastic material pressed between two much stiffer surfaces (e.g. molar-like tools) is proportional to the force applied and the contact area of the crushing tool, as long as the thickness of the target material is small compared with the diameter of the crushing tool. Thus, $F_{\text{crushing}} \propto D^2$, where D is the effective diameter or the square root of the molar area.
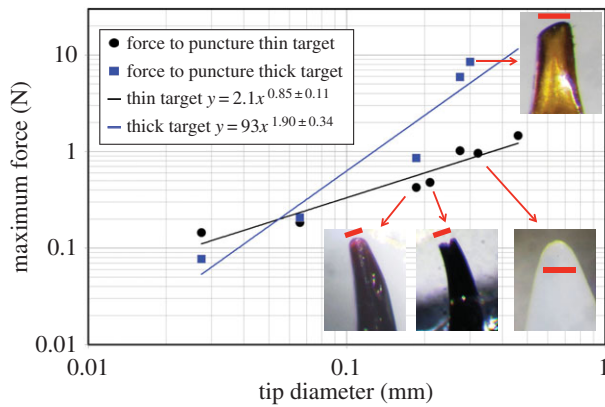
Figure 1. Force to initiate target fracture using different tools is consistent with the model. Cellophane, 0.038 mm thick, was used as a thin target (relative to tool tip diameters) and 2 cm thick acrylic polymer emulsion was used as the thick target. For the thin target, the fit exponent is 0.85 ± 0.11, consistent with an exponent of 1 (as expected) but not with an exponent of 0 ($p = 0.0002$) or 2 ($p = 0.00002$), and for the thick target, the exponent was consistent with 2 but not with 1 ($p = 0.03$). The inset pictures show, at the bottom from left to right, two scorpion stings and a salmon tooth, and at the top, a crab leg claw. The red bars show the estimated diameter of the contact region. This was based on observations suggesting that only the portion of the tip where the surface angle was greater than $20°$ from the long axis was in contact with the targets. The smooth and fractured stings of about the same tip diameter illustrate that the force depends more on diameter than the shape of the tip.

3.1.4. Implications for sharpness scaling in animals whose maximum force is proportional to the square of body length

We assume for our model that the maximum force that the animal can apply to the tool in order to puncture the target is proportional to the square of its body length (L), $F_{\max} \propto L^2$, and we apply this to the force versus diameter relations from above.

Thick target

Punch. Because $F_{\text{punch-thick}} \propto D^2$, and $F_{\max} \propto L^2$, we have $L^2 \propto D^2$ or $D \propto L$. Thus, we would expect the effective diameter of the contact region to be proportional to body length (isometry).

Cutting blade. Because $F_{\text{blade-thick}} \propto D$, and $F_{\max} \propto L^2$, we have $D \propto L^2$. For the thick target case, the diameter of the cutting blade edge has to decrease faster than would be expected from isometry in order for the smaller animal to cut a material that is at the force limit of the larger animal.

Thin target

Punch. To obtain the same stress from two different tip radii, $F_{\text{punch-thin}} \propto D$, and with $F_{\max} \propto L^2$, we expect $D \propto L^2$. Again, the tip diameter has to decrease faster than would be expected from isometry for two animal sizes to be able to produce the same maximum stress.

Cutting blade. For the blade on the thin target, $F_{\text{blade-thin}} = C$, and decreasing the diameter has no effect, because the stress is in a narrow band that moves out but does not change area with edge diameter.

Crushing tool. For molar-like crushing tools, $F_{\text{crushing}} \propto D^2$, and with $F_{\max} \propto L^2$, $L^2 \propto D^2$ or $D \propto L$. Thus, we expect the crushing area of the molar-like tools in phytophagous animals to scale isometrically.

Table 1. Force and energy to puncture thick and thin targets using different tools.

specimen number, species (source)	tool description	body length (mm)	diameter of tool tip (mm)	average force to puncture (Newtons)		average energy to puncture (Joules)	
				thin target	thick target	thin target	thick target
1. *Paruroctonus boreus* (collected)	scorpion sting	33	0.0274	0.14 ± 0.006	0.077 ± 0.006	$9 \pm 1 \times 10^{-6}$	$6 \pm 1 \times 10^{-6}$
2. *Hadrurus arizonensis* (Ken The Bug Guy)	scorpion sting	65	0.0658	0.18 ± 0.005	0.21 ± 0.04	$1.2 \pm 0.3 \times 10^{-5}$	$4.1 \pm 1.8 \times 10^{-5}$
3. *Hadrurus arizonensis* (Ken The Bug Guy)	scorpion sting	79	0.186	0.43 ± 0.02	0.86 ± 0.5	$3.0 \pm 0.3 \times 10^{-5}$	$4.4 \pm 0.6 \times 10^{-4}$
4. *Paruroctonus boreus* (collected)	scorpion sting	40	0.21	0.479 ± 0.0008		$3.4 \pm 0.2 \times 10^{-5}$	
5. *Oncorhynchus tshawytscha* (fishmonger)	salmon tooth	800	0.274	1.02 ± 0.03	5.9 ± 0.3	$1.0 \pm 0.1 \times 10^{-4}$	$6.5 \pm 0.7 \times 10^{-3}$
6. *Pachygrapsus crassipes* (collected)	crab tarsal claw	100	0.3		8.5 ± 0.5		$6.25 \pm 0.05 \times 10^{-3}$
7. *Oncorhynchus tshawytscha* (fishmonger)	salmon tooth	800	0.322	0.96 ± 0.04		$1.0 \pm 0.2 \times 10^{-4}$	
8. *Nereis brandti* (collected)	marine worm jaw tip	300	0.46	1.46 ± 0.06		$1.8 \pm 0.2 \times 10^{-4}$	
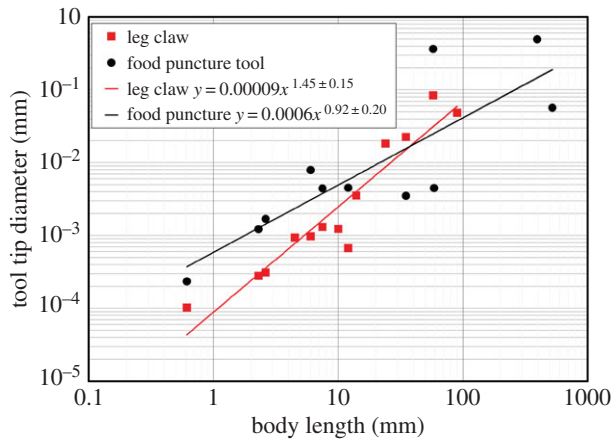
Figure 2. The scaling of the tip diameter for pristine tools (obtained before or just after moulting or birth). The exponent of the power law fit for food-puncturing tools was 0.923 ± 0.20, consistent with isometry, and for leg claws, 1.45 ± 0.15, greater than isometry ($p = 0.005$).

Figure 3. The energy (integral under the force displacement curve) to puncture thick and thin targets. For the thin Cellophane, the fit exponent was 1.09 ± 0.17, consistent with 1, but not with 0 ($p = 0.0004$) or 2 ($p = 0.0009$). For the thick acrylic polymer emulsion, the fit exponent was 2.88 ± 0.37, consistent with 3 but not with 2 ($p = 0.04$).

In summary, if our model animal is half as long as another, it can apply one-fourth of the force to its punch and can reach the same stresses in a thick target if the punch tip diameter is half (isometry), or, for a thin target, if the punch tip diameter is one-fourth (sharper than isometry). For a blade long enough that the contact length is the same in both animals, the half-length animal can apply the same stress to thick specimens if the edge diameter is one-fourth (sharper than isometry). For the blade on thin specimens, the smaller animal must reduce the length of the contact area in order to generate the same stresses. For crushing tools, the effective diameter of the total crushing area would be isometric with body length.
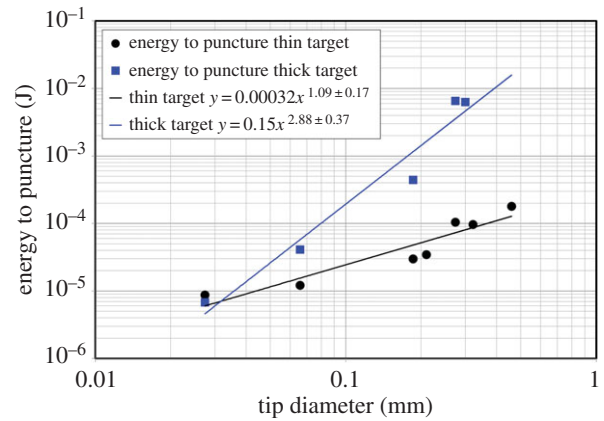
3.1.5. Scaling of pristine tool tip diameter with body length

Figure 2 summarizes the power law fits of the data from pristine tools in table 2 and shows that the diameter of the tool tips scales isometrically or steeper, as predicted by the model.

3.2. Tools with smaller diameters are more likely to fracture during cutting or puncture of a material

To the degree that smaller organisms can cut and puncture the same materials as larger ones, they require tools that can penetrate using less force. As we argue from force scaling above, the smaller model animal often requires tools even sharper than isometry would dictate. We argue here that sharper tools would be more susceptible to fracture, in the sense that the energy required to fracture the tool approaches the energy needed to penetrate the target as the tool diameter gets smaller.

Because of the complexity of fracture, it may be difficult to predict whether a tool will fracture before it cuts or punctures a certain target material. However, we suggest that the likelihood of tool fracture increases when the energy stored during cutting or puncture is a greater fraction of the energy required to catastrophically fracture the tool; that is, that the probability of fracture depends on the ratio of the maximum energy stored during puncture or cutting to the energy required to break the tool. A cut or puncture is initiated by pressing the tool into the target, storing energy in the elastic deflection of the tool and target that may be available to create new fracture surfaces, either in the target, as desired, or in the tool itself.

3.2.1. The minimum energy required to penetrate a layer increases with the diameter of the tool

The energy required to fracture is given by the energy required to break bonds and produce new surfaces; for isotropic materials, this fracture energy increases with the area of the new surfaces that are produced [11,12]. If the target membrane does not stretch much, then in order for the tool to penetrate, the bonds that need to be broken are, at a minimum, the bonds along the perimeter of the tool at maximum penetration. This perimeter is proportional to the effective diameter of the tool at maximum penetration, D. The energy to break these bonds is proportional to the area of the edge of this cylindrical plug that allows passage of the tool (figure 4). This surface area increases approximately linearly with the diameter of the tool at maximum penetration.

But even when the target membrane stretches, the minimum energy to puncture should increase, at least approximately, with the diameter of the punch. For example, when a 1.5 mm polycarbonate sheet was punctured with 6–12 mm steel balls, the sheet first developed a crack that extended from directly beneath the punch out radially in opposite directions past the edge of the punch, and then was stretched until the punch passed through the crack [17]. We would expect that the radial crack would have to increase in length according to the diameter of the punch, and thus the energy to make the crack would tend to scale with the diameter of the tool at maximum penetration.

3.2.2. Experimental test of the energy needed for a tool to penetrate a thin layer and initiate fracture in a thick layer

Figure 3 shows that the energy to puncture 0.038 mm Cellophane, over a 5 mm hole, with the natural punches of table 1, scaled linearly with the tool tip diameter.

Figure 3 also shows that the energy to initiate fracture in a thick specimen increased with the cube of the tool tip diameter. This is not the energy to penetrate clear through the material, just to pierce the surface by initiating fracture. It may be larger or smaller than the energy needed to produce the cracks that allow penetration completely through a layer.

Table 2. Sharpness of pristine tools as a function of body length.

organism	common name	tool	aspect ratio (L/W)	body length (mm)	tool tip diameter (mm)	source
leg claw equivalent						
Parasteatoda tepidariorum	sac spider (first instar)	tarsal claw	11.06	0.6	0.000102	collected and raised
Tapinoma sessile	sugar ant	tarsal claw	6.25	2.3	0.000279	laboratory colony
Wyeomyia smithii	mosquito	tarsal claw	3.43	2.6	0.000310	collected and raised
Vaejovis spinigerus	scorpion	tarsal claw	7.8	4.5	0.000936	Hatari Invertebrates, raised
Atta sexdens	leaf-cutter ant	tarsal claw	11.39	6	0.000973	lab colony
Hippodamia convergens	ladybug beetle	tarsal claw	5.86	7.5	0.00131	Carolina Biological, raised
Oncopeltus fasciatus	milkweed bug	tarsal claw		10	0.00123	Carolina Biological, raised
Armadillidium vulgare	pillbug	tarsal claw	6.9	12	0.000670	collected and raised
Tenebrio molitor	meal worm	tarsal claw	7.73	14	0.00356	Carolina Biological, raised
Pachygrapsus crassipes	shore crab	dactyl	4.93	24	0.0183	collected and raised
Libellula sp.	dragonfly	tarsal claw	8.91	35	0.0226	Carolina Biological, raised
Mus musculus	mouse	front R middle claw	7.3	57.9	0.084	Pet Smart
Cavia porcellus	guinea pig	front R middle claw	1.751	90	0.0486	Zany Zoo
food-puncturing tools						
Parasteatoda tepidariorum	sac spider (first instar)	marginal tooth	10.07	0.6	0.000234	collected and raised
Tapinoma sessile	sugar ant	distal mandibular tooth	4.28	2.3	0.00122	laboratory colony
Wyeomyia smithii	mosquito	labrum	34.80	2.6	0.00170	collected and raised
Atta sexdens	leaf-cutter ant	distal mandibular tooth	3.16	6	0.00796	laboratory colony
Hippodamia convergens	ladybug beetle	mandibular tooth	2.29	7.5	0.00442	Carolina Biological, raised
Armadillidium vulgare	pillbug	mandibular tooth	8.00	12	0.00451	collected and raised
Libellula sp.	dragonfly	mandibular tooth	2.67	35	0.00352	Carolina Biological, raised
Mus musculus	mouse	front incisor (FRI)	1.79	58	0.364	Pet Smart
Vaejovis spinigerus	scorpion	cheliceral tyne (prong)	5.67	59	0.00448	Hatari Invertebrates, raised
Sus scrofa	pig	front incisor	2.81	394	0.492	Carolina Biological
Squalus acanthias	mud shark	tooth	2.81	522	0.0566	Carolina Biological

3.2.3. The minimum energy required to fracture a tool increases with the area of the tool's cross section

If the material in the tool is isotropic, the energy required to fracture the tool is simply given by the area of the new surfaces. The minimum new surface area required to separate the tip from the rest of the tool is the cross-sectional area at the separation point. Of course, the tip rarely breaks at a perfect cross section, but we suggest that, for a given applied force, the likelihood of tool fracture increases as this minimum fracture energy decreases.

As an aside, in our model, fracture of the tool causes an increase in the energy required to cut or puncture only when the fracture increases the diameter of the tool at maximum penetration. So breaking the rounded tip off a cylindrical tool that must penetrate past the rounded tip into the cylindrical portion of the tool will not increase the puncture energy. Breaking the tip off a conical tool would increase the puncture energy because, in order to reach the same depth, a wider portion of the tool must penetrate the target. The importance of diameter over shape is supported in the data of table 1, figures 2 and 3. As illustrated in figure 1, specimens 3 and 4 have about the same tip diameter, but specimen 4 is a sting from a much smaller scorpion, fractured in nature far enough up the sting that the diameter of the broken tip was about the same as the diameter of the undamaged smooth-tipped sting from a larger species of scorpion. The force and energy required to puncture was about the same for these very differently shaped tips of about the same diameter.

3.2.4. Smaller-diameter tools have a higher ratio of minimum tool fracture energy to minimum penetration energy and are thus expected to be more likely to fracture

The minimum energy required to fracture a tool at a cross section is proportional to the area of the cross section, so tools with lower cross-sectional areas require less energy to catastrophically fracture (assuming that the tools are made of the same material), and the minimum energy increases with D^2. At the same time, the minimum energy required to make the puncture hole increases according to the circumference of the tool (figure 4) or D. Thus, a tool with one-half the diameter of another would require about one-half of the energy to puncture the target layer, but would require only one-fourth of the energy for the tool to fracture in two. The ratio of the D^2 dependence of tool fracture energy to the D dependence of puncture energy results in this proposed indicator of resistance to tool fracture increasing $\propto D$.

The proposed indicator is only useful if the typical energy required to fracture the tool and the typical energy to puncture the target are proportional to the minimum energy required. An alternative hypothesis would be that the stored energy is dominated not by the energy required to penetrate the target, but by the energy required to reach the failure stress levels (see §3.2.2). In this case, the indicator of fracture resistance would still scale with the tool diameter, $\propto D$, for the thin target in 3.2.2 (because the required energy increased with D) but not for the tested thick target. Realistic tests of fracture for real tools that are
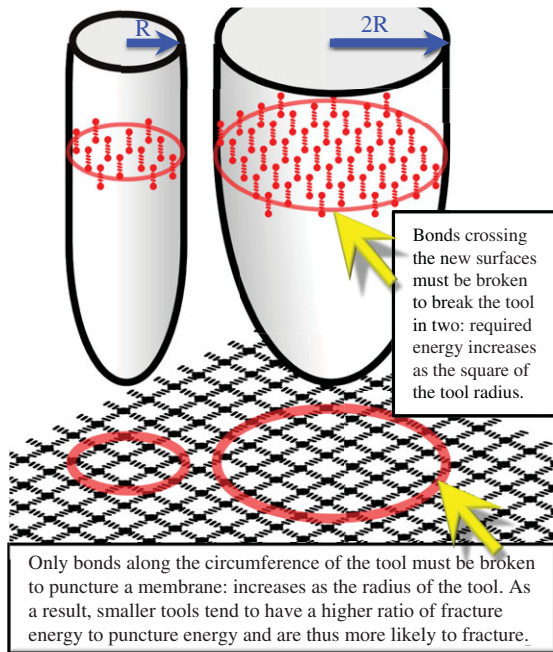
Figure 4. The minimum energy to fracture the tip off a punch-like tool scales with the square of the diameter, while the minimum energy to puncture scales with the diameter.

approximately isometric and made of similar materials would test the hypothesis that the ones with the smaller-diameter tips are more likely to fracture while puncturing similar materials.

The hypothesized trend towards greater fracture susceptibility in smaller tools could be overcome if smaller tools employed more fracture-resistant materials. For our example with a factor of 2 difference in tool diameter, the smaller tool required one-half of the energy to puncture and one-fourth of the energy to fracture the punch. Thus the ratio of the two energies could be maintained if the energy of fracture, K (joules required to produce a crack of unit area) was twice as large so that the fracture energy of the smaller tool was one-half rather than one-fourth. Thus there may be a tendency for the energy to fracture per unit area, K, of materials used in cutting and puncturing tools to be related to the tool diameter at maximum penetration, D, by $K \propto 1/D$.

3.3. Force limitations also are likely to lead to higher aspect ratio tools, which tend to store energy at higher densities, making the tools even more susceptible to fracture

3.3.1. Smaller organisms are more likely to have higher aspect ratio tools

While a smaller organism may overcome its lower maximum force by using tools with smaller tip radii, the distance that the tools must penetrate may be the same as for larger organisms, resulting in higher aspect ratio (the length of the tool divided by the diameter) tools in smaller organisms. Figure 5 illustrates this, showing that if two organisms must both penetrate the same membrane, then both tools must be at least as long as the membrane is thick. If the smaller animal must use tools with lower cross-sectional area to overcome force limitations, then the aspect ratio would be greater
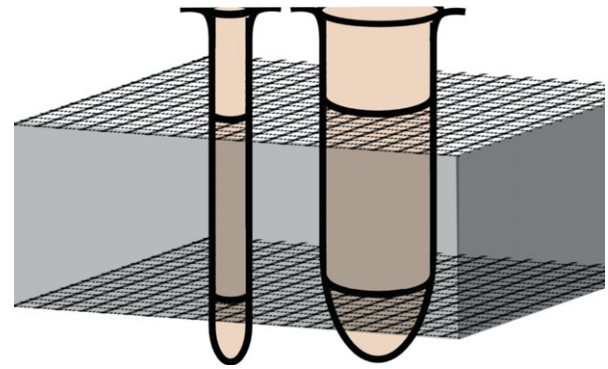
Figure 5. A smaller organism can use a smaller-diameter tool to puncture a target with less force, but the aspect ratio will be greater than the minimum possible aspect ratio for the larger-diameter tool.
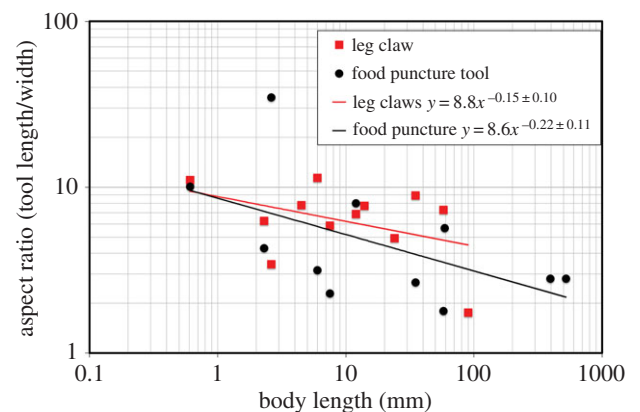
Figure 6. Aspect ratios of tools in table 2. For food-puncture tools, the exponent of the fit is -0.22 ± 0.11, and the probability that the slope could be zero (isometry, because we are plotting the ratio of two lengths) is $p = 0.039$. For the leg claws, the exponent is -0.15 ± 0.10 ($p = 0.088$). Comparable higher aspect ratio tools store more energy, which may make fracture more likely.

(longer and thinner) than a larger-diameter tool that was also just long enough to penetrate.

3.3.2. Aspect ratios for pristine tools as a function of body size

Figure 6 shows the aspect ratios of tools listed in table 2. The aspect ratios of the food-puncturing tools tend to decrease with body length ($p = 0.04$), steeper than isometry.

3.3.3. Energy stored in a model tool from forces bending or compressing the tool

3.3.3.1. Energy stored in bending

The energy stored in a cylinder of a certain length subjected to a transverse force at the tip (that bends the cylinder), is, according to beam mechanics, $U_{stored-bending} \propto F_{bending}^2/D^4$ (where $U_{stored-bending}$ is the energy stored from bending, $F_{bending}$ is the bending force and D is the diameter of a cross section of the tool). If accidental lateral forces are proportional to the axial force producing the penetration, as we would expect, then the accidental lateral force would be proportional to the tool diameter, $F_{bending} \propto D$ (because the purposefully applied force to puncture is proportional to D), so the energy scaling would be $U_{stored-bending} \propto 1/D^2$. Thus for two tools that are of the same length, but one is of

Table 3. Summary of scaling relations for puncture, cutting and crushing tools.

	force required to produce a given stress		tool tip diameter D, assuming equal stress and maximum force proportional to square of body length (L)		minimum energy to fracture tool/ minimum energy to penetrate target	energy stored in tool/ energy to fracture tool	
	thick target	thin target	thick target	thin target		bending	axial compression
punch	$F \propto D^2$	$F \propto D$	$D \propto L$	$D \propto L^2$	$\propto D$	$\propto 1/D^4$	$\propto 1/D^2$
blade	$F \propto D$	$F = C$	$D \propto L^2$	no change with L	$=$ constant		
crushing surface		$F \propto D^2$		$D \propto L$	$\propto D$		

half the diameter of the other, puncturing the same material, the smaller one will store four times more energy than the larger tool from lateral forces, while it requires one-fourth the energy to fracture in two. Thus, the ratio of energy stored to energy required to fracture is $U_{\text{stored-bending}}/U_{\text{fracture}} \propto 1/D^4$.

3.3.3.2. Energy stored in compression

The energy stored in compression along the main axis of the cylindrical tool is $U_{\text{stored-compression}} \propto F_{\text{axial}}^2/D^2$. Because the force required to reach the fracture stress threshold is proportional to the diameter of the tool, $F_{\text{axial}} \propto D$, $U_{\text{stored-compression}} \propto 1$, and the energy does not depend on D. The same amount of energy would be stored in compression during puncture by two tools of the same length but of different radii. However, because the energy required to fracture the tool is proportional to D^2, the ratio of the energy stored during puncture to the energy required to fracture is $U_{\text{stored-compression}}/U_{\text{fracture}} \propto 1/D^2$. Thus, for a given tool material and length, the smaller-diameter tools will tend to store more energy in bending, whereas the larger diameter tools store relatively more in compression.

3.3.4. Energy stored in tool bending and compression may be available for fracturing the tool or target

We have argued that higher aspect ratio tools are more likely to store energy comparable to or greater than the energy needed to fracture the tool. If the modulus of elasticity were higher so that the tool deflected less and stored less energy, or if the fracture energy were higher, the trend towards a greater danger of fracture in higher aspect ratio tools would be countered. One might thus expect more fracture resistance and higher modulus of elasticity materials in the shafts of the tools of smaller organisms. In order to keep the same ratio of energy stored as the tool bends for two different tools of the same length but with diameters that differ by two (aspect ratios differ by two), $KE \propto 1/D^4$, where K is the energy of fracture, E is the modulus of elasticity and D is the diameter of the tool.

In summary, for two tools that are the same length and made of the same materials, but differ by a factor of two in aspect ratio, the ratio $U_{\text{stored-bending}}/U_{\text{fracture}}$ would be 16 times greater for the specimen with the higher aspect ratio. In order for this ratio to remain the same, the smaller tool could be made from a material for which the product of K and E would be 16 times greater. This is a large factor, and unlikely to be achievable, especially for aspect ratios that differ by

more than a factor of two. It seems likely that small animals need to take extra care when puncturing to apply forces only perpendicular to the target in order to avoid bending the tool.

The energy stored in higher aspect ratio tools during puncture is closer to the energy required to break the tool, but is also closer to the energy required to puncture the membrane for smaller tools. Thus, if a small organism cannot supply the force to store the required puncture energy in the 'springiness' of the target membrane, it might store the energy in more compliant bending of the tool. This may explain the curvature of the sting of a scorpion, which appears designed to store energy for the puncture without the energy being available in the regions of lowest cross section that are at the greatest fracture risk. The curvature of the scorpion sting (and a cat's claw) is such that, in normal use, the bending moment is small in the small-diameter region near the tip, but is large in the larger-diameter region near the base of the sting. The energy stored in bending is mainly near the base of the sting and, if the sting is held perpendicular to the target, most of the energy is available to puncture the target but is not available to bend and fracture the tip. The energy stored in the bending of the sting base may compensate for the lower power of the smaller animal and rapidly provide energy to complete the penetration of the target.

4. Conclusion

4.1. Summary of scaling relations

Table 3 is a summary of the scaling relations discussed here for the homogeneous linear elastic model of tool–target interactions. It shows the relations between the effective diameter (square root of the area in the absence of cylindrical symmetry), D, of the tool at the border of the contact region between the tool and the target, and F, the force that must be applied to produce a certain stress, and L, the effective length of the animal, assuming that maximum force scales as length squared, $F_{\text{max}} \propto L^2$. The table also provides the relations between D and energy ratios that may be related to the likelihood of fracture. Thick and thin targets are defined relative to the tool diameter, D.

4.2. Some implications of size effects in cutting and puncturing

(1) Smaller animals are likely to employ more fracture-resistant materials. If different materials are employed,

we would expect that the energy required per unit area of a new surface, K, would tend to be related to the diameter (D) of the tool as $K \propto 1/D$.

(2) As the aspect ratio of the tool increases in order to overcome force limitations, the storage of energy that may help fracture the tool can be kept the same if $KE \propto 1/D^4$. Of course, this scales so fast that it is unlikely that materials will be available that meet these requirements. Thus other compensation mechanisms (some discussed below) are likely.

(3) Behaviour that reduces lateral forces may be more likely in smaller animals. For example, immobilization of the prey or other ways of reducing relative motion between the tool and the target may be more likely. Smaller animals may be more likely to carefully adjust the tool angle to be perpendicular to the target surface in order to minimize bending. At the same time, the prey strategy may more likely include rapid motions that might lead to fracture of the predator's tool.

(4) Smaller animals may tend to cut or puncture more slowly than larger animals, both to reduce accidental lateral forces and because the energy that they can spend per second making new fracture surfaces is much lower, scaling roughly with the cube of the body length [18].

(5) Smaller animals may be more likely to use stored mechanical energy for aiding target fracture, because their power output is much lower. Possible examples include the curved sting of the scorpion and the trap jaws of some ants.

(6) Smaller organisms may be more likely to have replaceable tools, like the radula of molluscs. Similarly, some may have a higher moulting rate, more rapidly replacing damaged tools [4]. High aspect ratios can, in some cases, be avoided using 'self-sharpening' mechanisms.

(7) Smaller organisms may be more likely to use multiple materials in their tools with different balances of mechanical properties in order to minimize the chance of fracture. For example, they may be more likely to use hard caps on more fracture-resistant shafts. The heavy-element biomaterials employed by many small organisms in different regions of their tools [1,19–21] may

serve to precisely control mechanical properties. Levels of hydration may also be controlled to precisely tune mechanical properties [22].

(8) Slice–push techniques [3], which reduce blade contact area or otherwise reduce the forces needed to cut, may be more common in smaller organisms. An example would be the V-blade in leaf cutter ants [23].

(9) This analysis also applies to the effects of wear. As usage increases the diameter of the tools by wearing away regions with lower diameter, greater forces are required, scaling with the diameter according to table 3. Average natural wear increases the force and energy required of leaf cutter ants by a factor of about two [23].

(10) The prediction of molar isometry is supported in mammals [6]; we hypothesize that isometry would extend to the molar-like processes of insect mandibles [5].

(11) We did not address shearing, in the sense of scissors-like cutting, which is less common among smaller animals [4]. Scaling of shearing may be obtained for models that are analogous to those used here.

(12) Of course this analysis applies to human-made tools as well. Certain small tools may be force-limited and so require sharp tips or edges, but even a tool made of the strongest materials will fracture on a soft target if the diameter is small enough.

(13) Tool damage and wear are more likely to be life-threatening to smaller animals because small animals are less likely to be able to use brute force to overcome broken or highly worn (an accumulation of non-catastrophic fractures) tools.

(14) Because tool damage from fracture may be more consequential for smaller animals, it may limit lifespan after the last moult. Leaf cutter ants with average wear cut roughly half as fast and spend roughly twice the energy as their younger sisters with pristine mandibles. This loss of efficiency may help explain why workers live for months, whereas queens can live for more than a decade [23].

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