

# Leaf-cutter ants with worn mandibles cut half as fast, spend twice the energy, and tend to carry instead of cut

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**Abstract** The importance of mechanical wear in the behavioral ecology and energetics of small organisms is an open question. We investigated wear in leaf-cutter ants, *Atta cephalotes*, because their cutting technique can be imitated and the leaves are the main energy source for the colony. We found that a razor-sharp (50-nm radius) “V-blade” that cuts leaves between the first and second mandibular teeth was dulled (~10- $\mu$ m radius) and often nearly worn away on foragers. We found that the force required to cut standard leaves, using mandibles removed from foragers cutting in the wild, varied by a factor of 2.5 with tooth wear, defined as the difference between pupal and actual tooth length. We also found that wear significantly reduced the cutting rate. From the distribution of wear among the cutting foragers, we estimated that the wild colony would have spent 44% less of both energy and time making the observed cuts if the cutters’ mandibles had all been pristine. Finally, wear correlated with behavioral differences—foragers with the most worn 10% of mandibles almost exclusively carried rather than cut. This previously unreported form of task partitioning suggests that eusociality may extend useful lifespans by making it

possible to switch tasks as skills decline. We developed a model, assuming that ants do work at a constant rate proportional to their mass, to predict the cutting rate from head width, tooth wear, and force to cut leaves with a scalpel ( $R=0.62$ ), and we used this estimate to argue that the partitioning of cutting and carrying was sub-optimal but better than random. Wear’s strong effect on performance may promote wear-avoiding behavior and wear-resistant mandible composition; it may affect leaf selection and worker lifespan and it raises the possibility that wear is a similarly important constraint for many other small organisms.

**Keywords** *Atta cephalotes* · Task allocation · Energetics · Cutting rate · Wear · Task partitioning · Aging

## Introduction

Only a few reports have quantified the effects of wear on small organisms (Chapman 1964; Raupp 1985; Roitberg, Gillespie, Quiring, Alma, Jenner, Perry, Peterson, Saloman and VanLaerhoven 2005) and these have not investigated the costs of normal levels of wear in the wild. We have recently suggested that wear damage and particularly fracture of “tools” such as claws and teeth tend to be greater problems for smaller organisms (Schofield, Niedbala, Nesson, Tao, Shokes, Scott and Latimer 2009). One reason for this is that smaller organisms can be subjected to the same forces from the environment, predators, and prey as larger organisms but tend to have structures with smaller cross-sectional areas. In this paper, we used leaf-cutter ants to test the prediction that typical levels of wear strongly affect the efficiency (and thus the fitness) of small organisms.

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Leaf-cutter ants harvest fresh leaves that provide energy directly to adults from sap and indirectly to the brood and adults through a symbiotic fungus grown on the processed leaves (Quinlan and Cherrett 1979; Wirth, Herz, Ryel, Beyschlag and Hölldobler 2003; Hölldobler and Wilson 2009). Leaf cutting may be the ants' most energy-intensive activity (Roces and Lighton 1995). The mandibles are used asymmetrically to slice the leaves, with the lagging mandible often held at a nearly fixed orientation in the cut, while the leading mandible opens and closes (Tautz, Roces and Hölldobler 1995). For most of the cut, the long distal tooth of the lagging mandible penetrates just beyond the leaf surface opposite from the ant such that the surface ("Electronic supplementary material", movie 1: <http://www.youtube.com/watch?v=FMsqTRCHHWI>), and, for larger ants, the entire thickness of the leaf is cut between the distal and second tooth. The lead mandible is used as a temporary anchor or to partially or completely cut through the leaf in advance of the lagging mandible ("Electronic supplementary material", movie 2: <http://www.youtube.com/watch?v=VqOsOWjKQs>). On thicker veins, the two mandibles are employed with increasing symmetry and cut with a sawing motion ("Electronic supplementary material", movie 2: <http://www.youtube.com/watch?v=VqOsOWjKQs>). From the field data in this study, 22% of the leaf cutting time was spent cutting large veins (defined as the central vein or a branch directly connected to the central vein), which we analyzed separately from off-vein cutting because different teeth are employed.

The rate at which energy is obtained for the colony depends on the leaf cutting rate. Most studies have found that the cutting rate increases with the size of the ant (Howard 1988; Nichols-Orians and Schultz 1989; Burd 1996) and decreases with leaves that are more mature or have a higher areal density (Wilson 1980; Nichols-Orians and Schultz 1989; Roces and Hölldobler 1994; Burd 1996). To evaluate the cutting difficulty, leaves have been tested using penetrometers and instrumented scissors (Tanton 1962; Nichols-Orians and Schultz 1989, 1990; Clark 2006). In one study, a threefold increase in penetrometer toughness was associated with a threefold reduction in cutting rate, suggesting a possible linear relationship between force and cutting rate (Nichols-Orians and Schultz 1989). Our observations suggest that most of the work is done in slicing, so we developed an instrument that measures the force required to slice a leaf with a scalpel or an ant mandible.

This instrument was used to test the hypothesis that typical levels of wear significantly increase the force and energy required to cut leaves, and we used field observations to test the hypothesis that wear significantly increases the time required to cut leaves. Because mandibular wear would reduce the cutting efficiency but not carrying efficiency, we also tested the hypothesis that ants with worn mandibles tend to carry instead of cut.

## Materials and methods

### Specimens

We used our several-year-old colony of *Atta cephalotes* at the University of Oregon to obtain pristine mandibles, for cutting rate comparisons with the field colony, and to develop field techniques. Cutting rates were measured on medium-aged Himalayan blackberry (*Rubus armeniacus*) leaves placed in the foraging terrarium. We used stage 4 pupae (all cuticle darkening [Schofield, Nesson and Richardson 2003]) to determine pristine mandibular tooth length. To obtain fully developed pristine mandibles that were used to measure cutting energy, we isolated pupae in a chamber with an entrance too small for them or leaf disks to pass through, but large enough for smaller nurse ants. The mandibles were taken when the isolated ants were at least 100 h post-eclosion to ensure that the teeth contained a full complement of zinc (Schofield, Nesson and Richardson 2003).

Field data were collected from a single *A. cephalotes* colony in Soberania National Park, Panama, along the Camino del Oleoducto, 8.1 km from the gate at Gamboa. Data were collected at night in February and March of 2007 since there was little daytime foraging activity during this dry season. We observed the colony foraging on the vine *Odontadenia macrantha* (identification: Carmen Galdames, Smithsonian Tropical Research Institute), even though the sap is latex-like (Stradling 1978), and selected this species to fill an artificial tree (Wetterer 1991) that we constructed from polyvinyl chloride tubes to provide easy observer access. The four-legged "tree" was set up about 2 m from a trunk foraging trail, about 85 m from the nest. Each night, part of a fresh *O. macrantha* vine, with marked leaves, was laid across the trunk trail and, when ten or more ants were cutting, the vine was placed in the artificial tree, with a portion trailing to the ground. We began collecting data once a continuous trail of ants was established from the trunk trail up into the artificial tree.

### Cutting observations

Cutting was timed using stopwatches and began and ended when the ant was about a mandible length from each endpoint because of the variability in initiating and terminating the cut (e.g., when the ant manipulates the disk to catch it). Any time spent cutting the central vein or a vein directly connected to the central vein was recorded separately because observations suggested that different teeth were important for vein cutting.

After cutting, the ant was placed in a vial in an ice-filled chest and the leaf disk was taped on a watercolor paper tablet, with identifying markings. Timing data, the leaf

number, the number of ants on the leaf, and which mandible lagged were recorded. Temperature and time of night were also recorded at intervals. The observers used breathing apparatuses with one-way valves to direct exhaled carbon dioxide through a tube and away from the ants. The observers did not wear an insect repellent during the collection of data for all but 14 of 79 ants, and no significant cutting rate difference was noted for these 14.

#### Measurements of the force to cut leaves

After one to several ants had cut disks from a leaf, the remaining portion of the leaf was removed and the force required to cut regions free of first- and second-order veins with a No. 11 surgical blade (Feather Safety Razor Co., Osaka, Japan) was measured using the field apparatus described below.

To test that the cutting forces for *O. macrantha* leaves were not highly anisotropic, the cutting forces were measured both parallel and perpendicular to the central vein for some leaves. The force in the parallel direction was significantly larger than in the perpendicular direction, but the means differed by a factor of only 1.2 (Wilcoxon matched-pairs signed-ranks test,  $n=12$  pairs,  $p=0.04$ ). An average of perpendicular force values from three regions of each leaf was used to compare the leaves and for the correlation analysis.

To reduce the number of variables affecting cutting rate, we selected similar *O. macrantha* leaves, resulting in similar cutting forces ( $0.14\pm 0.03$  N) and in no significant correlation between cutting rate and force to cut the leaf. However, for predicting the cutting rate of the wild colony from the laboratory colony, accounting for the fourfold force difference between the two types of leaves was essential.

#### Measurements of cutting distance and vein diameter

Measurements of the cutting distance were made using Camoy image analysis software (The Laboratory of Plant Systematics, K.U. Leuven, Leuven, Belgium) after the sheets holding the leaf disks were scanned and digitized. No shrinkage correction was made since we found that the monitored disk perimeters of *O. macrantha* shrank by less than 2.5% in a year.

The diameters of the cut veins were measured using “Image J”, version 12.0.0, analysis software (National Institutes of Health, (<http://rsbweb.nih.gov/ij/index.html>)). The vein cutting rate was calculated as the ratio of the square of the vein diameter to the time spent cutting the vein ( $\text{m}^2/\text{s}$ ).

#### Measurements of mandible wear

Frozen ants were decapitated under water, photographed using a Nikon Coolpix 4500 mounted on a Zeiss dissection

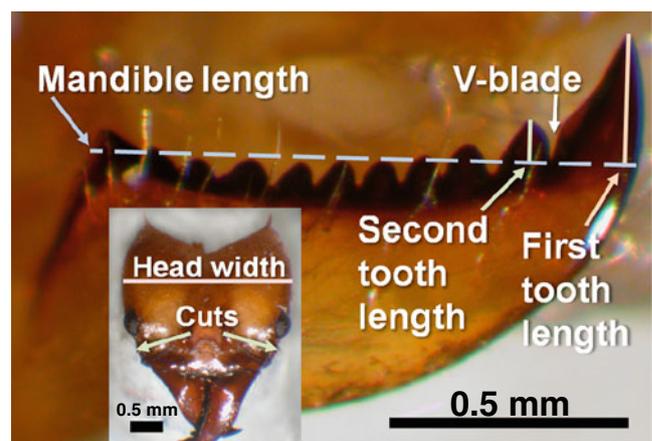
microscope, and the images were measured using “Image J”. In order to open the overlapping mandibles without damaging the teeth, we inserted a scalpel blade just posterior of the clypeus and cut the mandible closer apodemes as diagrammed in Fig. 1. When the mandibles were open, the head was oriented in a clay holder so that the flat anterior face of the photographed mandible would reflect back a light shining into one of the microscope eyepieces, minimizing distortions in the photographs due to perspective.

The measured features are shown in Fig. 1. We defined the head width as the greatest distance across the head in a line parallel to the line connecting the eyes. The mandible length was taken as the length of the line connecting the proximal and distal edges of the mandible, passing through the bottom of the most distal and most proximal tooth gap valleys. The length of the first (most distal) and second tooth on each mandible was taken as the distance from the line giving the mandible length to the tips of the teeth.

To estimate the precision of the mandible measurements, the procedure of mounting, photographing, and measuring was performed by three different investigators on a single ant repetitively for a total of ten procedures. The standard deviations of the 20 values (left and right) for the first and second teeth were 0.013 mm (7%, 31%) and 0.008 mm (13%, 40%) respectively, where the first parenthetical value is the percentage of the average length and the second is the percentage of the standard deviation of lengths for all ants in the field study.

#### Carriers

In order to compare the wear levels of cutters and carriers, we collected, at multiple times on different days, every ant



**Fig. 1** The measurements used in this paper are indicated on a pristine mandible of a late-stage pupa, head width 2.6 mm, and, in the inset, a forager, head width 2.9 mm. Also indicated are the cuts used to open the mandibles and the V-shaped blade, formed by processes of the first and second tooth, employed in off-vein leaf cutting

carrying a leaf disk away from the artificial tree as it crossed a line just before the junction with the trunk trail until a pre-specified number of ants had been collected. We compared these to the cutters discussed above. To prevent any artifacts from size distribution differences, we limited the range of mandible lengths (1.00–1.35 mm), split this range into bins with 0.05-mm spacing, and ensured an equal number of cutters and carriers in each size bin by randomly discarding members of the overrepresented group.

To determine if carriers and cutters were different populations, we followed seven ants observed cutting and found that in every case the cutters dropped (one ant) or directly transferred (six ants) the leaf disk to another ant before they reached the trunk trail. This is a higher proportion of direct transfer than the 9% that has been observed at the base of a source tree for *Atta colombica* (Hart, Anderson and Ratnieks 2002), but it may be that many transfers take place in the tree before the ants reach the ground.

#### Blind analysis

All decisions on measures of wear, data cuts, regression models, and tests for significance were made before any statistical analysis or plotting of cutting rate against wear.

#### Wear figures of merit

In harvester ants, wear has been quantified by counting the remaining teeth (Oettler and Johnson 2009), but *A. cephalotes* do not tend to lose teeth. Our measures of wear were based on the differences between the tooth lengths and the un-worn lengths calculated from the fit of pupal data in Fig. 2. We used only the two most distal teeth because of a large scatter in the lengths of the more proximal pupal teeth.

For off-vein cutting, the first tooth on the leading mandible and the second tooth on the lagging mandible were observed to play a major role (“Electronic supplementary material”, movies 1: <http://www.youtube.com/watch?v=FMsqTRCHHWI> and 2: <http://www.youtube.com/watch?v=VqOsOWjLKQs>), so the wear figure of merit ( $W_{\text{off-vein}}$ ) was defined as:

$$W_{\text{off-vein}} = (\Delta T2_{\text{lagging}} + 0.38\Delta T1_{\text{leading}})/2, \quad (1)$$

where  $\Delta T1_{\text{leading}}$  and  $\Delta T2_{\text{lagging}}$  are the differences between the measured lengths and the estimated pupal lengths for leading mandible tooth 1 and lagging mandible tooth 2, respectively. The equalizing weighting factor, 0.38, was the ratio of averages of  $\Delta T2_{\text{lagging}}$  and  $\Delta T1_{\text{leading}}$ .

For vein cutting, both mandibles were used symmetrically so all four teeth were used in the wear figure of merit ( $W_{\text{vein}}$ ):

$$W_{\text{vein}} = (\Delta T2_{\text{leading}} + \Delta T2_{\text{lagging}} + 0.38(\Delta T1_{\text{leading}} + \Delta T1_{\text{lagging}}))/4. \quad (2)$$

Finally, only the lagging mandible was tested by our apparatus, so the wear figure of merit for this study was simply:

$$W_{\text{lagging}} = \Delta T2_{\text{lagging}}. \quad (3)$$

We investigated an alternative measure of wear, the radius of the proximal blade on the first tooth of the lagging mandible, measured using scanning electron microscopy, and found that it was well correlated (Pearson’s correlation,  $n=9$ ,  $r=0.73$ ) with the wear figure of merit used for off-vein cutting ( $W_{\text{off-vein}}$ ).

#### Data cuts

Field data for specific ants were eliminated for the following reasons: the four teeth were not similarly worn, suggesting catastrophic fracture (seven ants; eliminated if the range of values for terms in  $W_{\text{vein}}$  exceeded 0.046 mm), head widths were outside the range of 2.2 to 3.5 mm (six ants), a timing error (one ant), a leaf marking error (one ant), and an outlier (Grubb’s test, 0.05 level) in cutting rate (one ant). Together these cuts reduced the total for off-vein cutting from 95 to 79 ants (eliminated 17%) and for vein cutting from 33 to 31 (eliminated 6%).

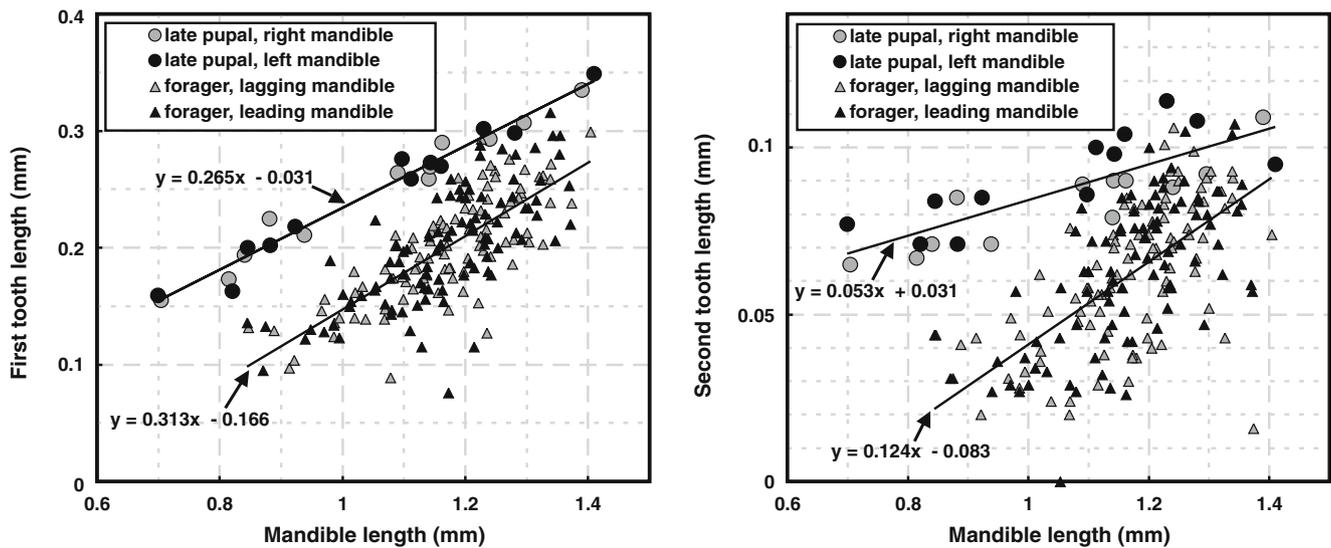
#### Regression models

Before examining the relationships between cutting rate and wear (“un-blinding”), the relationships between other pairs of variables were examined. We found that faster-cutting, large ants tended to have less wear than smaller ants, as evident in the right-hand plot of Fig. 2 (Pearson’s correlation between mandible length and wear,  $n=79$ ,  $r=-0.47$ ,  $p=0.00001$  for the off-vein cutting data set). To avoid the bias this would introduce, we chose to test the wear hypothesis using multiple regression models instead of simple correlations.

We used the following model in which the off-vein cutting rate ( $R_{\text{off-vein}}$ ) is a function of head width ( $H$ ), wear ( $W_{\text{off-vein}}$ ) and an interaction term multiplying head width and wear:

$$R_{\text{off-vein}} = A_0 + A_1H + A_2W_{\text{off-vein}} + A_3HW_{\text{off-vein}}. \quad (4)$$

We included an interaction term (Aiken and West 1991) so that wear could result in a smaller reduction in cutting rate for small slow ants than for large fast ants. Because the slopes of cutting rate as a function of wear can be greater



**Fig. 2** The distributions of first (*left plot*) and second (*right plot*) tooth lengths vs. mandible length for foragers (*triangles*) of the field colony and pupae (*circles*) of the laboratory colony of *A. cephalotes*. The difference in length between a forager's tooth and the pupal length, given by the line fit to the pupal data, was used as the measure of wear. The average wear of the first tooth is roughly independent of mandible length (the fit lines are nearly parallel), but the second tooth tends to be more worn in smaller, slower cutting ants, a potentially biasing trend that we accounted for using multiple linear regressions.

for larger ants, the significance level can vary with head width.

For vein cutting, we found a large spread in cutting rates (a factor of 30), so we fit the natural logarithm of cutting rate:

$$\ln(R_{\text{vein}}) = B_0 + B_1H + B_2W_{\text{vein}}. \quad (5)$$

Because of the logarithm, the slope of the fit curve increased with increasing head width so an interaction term was not used.

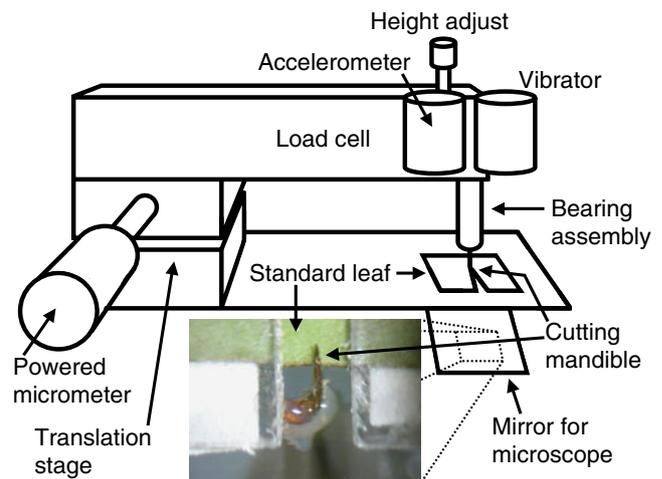
Correlation and multiple linear regression analysis software were written using MatLab (<http://www.mathworks.com/>) "corr", "regress," and "regstats" functions.

Instrument for measuring the work required for a mandible to cut a leaf

An apparatus was built to measure the work required to cut leaves with dissected mandibles (Fig. 3). A mandible was attached in the normal cutting orientation to a bit using 5-min epoxy gel (Devcon, [www.itwconsumer.com](http://www.itwconsumer.com)). The adhesive was cured for at least 12 h at 39°C. The bit with the attached mandible was mounted in a chuck that was attached to the load cell of the testing machine using a ball bearing assembly that allowed the off-set mandible to swivel freely and self-align. The load cell was custom-made

The difference between the two teeth in wear as a function of ant size may be accounted for by tooth shape: the similar and constant angled cones of a small and a large first tooth have similar cross-sections as a function of distance from the tip and so should wear similarly for similar challenges. The second tooth has a cone angle that decreases with distance from the tip, so the cross-section of a smaller tooth of the same shape would be smaller for an equal distance from the tip, resulting in faster wear

using four strain gauges (Vishay Micro-Measurements, Raleigh, North Carolina) and was attached to an optical translation stage (model 400, Newport Co., Fountain Valley, CA, USA) that was driven by a powered micrometer (Oriel, Stratford, Ct.) with the extension measured to within 0.1  $\mu\text{m}$  using a shutter on the micrometer shaft. The load cell and micrometer signals were recorded by a computer. The data for the extension of the micrometer were corrected in software for machine compliance in order



**Fig. 3** Apparatus for measuring the force required to cut a leaf with a dissected mandible

to give the actual motion of the mandible. The compliance of the apparatus (dominated by the load cell) was calculated using the recorded extension of the micrometer as a function of force when the mandible holder was kept from moving by an inserted block.

The testing apparatus was equipped with a vibrator and an accelerometer in order to investigate the effect of vibrations that imitated stridulation (Tautz, Roces and Hölldobler 1995).

#### Standard leaves

We selected leaves of the Portuguese laurel cherry, *Prunus lusitanica*, for measurements of the work required to cut because they were uniform in thickness, had relatively small higher-order veins, were resistant to drying, and were readily available as an ornamental on campus. Each leaf was cut into segments, four of which were tested by cutting with a scalpel and eight others used to test two mandibles. The between-leaf variation for the scalpel forces was similar to the within-leaf variation so we did not normalize the mandible forces using the scalpel data. Leaf segments were stored above-water in a closed container until tested. The *P. lusitanica* leaves were similar to the *O. macrantha* leaves, used for the field colony, in force required to cut with a No. 11 scalpel (averaging 0.16 and 0.14 N, respectively), and they were both fairly thick (averaging 0.25 and 0.13 mm, respectively).

#### Testing procedure

The mounted mandible was aligned horizontally, using a microscope and mirror assembly, with a ~0.25-mm notch cut in the leaf to help initiate the mandible cut, and aligned vertically so that the long first tooth would run along the underside of the leaf. The cutting sequence for mandibles began with a 3-mm pre-leaf segment to determine the zero-force level. The measurement segment was another 3-mm stretch that began 2 mm after the mandible touched the leaf (in order to avoid the large force variations at the beginning of the cut). The work required to cut the 3-mm segment of the leaf was obtained by numerically integrating the area under the compliance-corrected force–displacement curve. The distance-averaged force was obtained from this work by dividing by 3 mm. The strain gauges were sensitive to room temperature fluctuations, so a force calibration was typically made immediately before and after two or three mandible measurements, using a mass that was attached to the mandible holder with a string and hung using a ball bearing pulley. The calibration was made with the powered micrometer running at the same extension used for the cutting data.

Instrument for field measurements of the force required to cut a leaf with a scalpel blade

The instrument described above was used in modified form for field measurements: a less stiff load cell was used to minimize the required signal amplification, the apparatus was powered by a battery, and a hand-powered micrometer was used to drive the scalpel blade, which was mounted in a different chuck. The voltage was read by eye from a battery-powered multi-meter as the scalpel cut over a distance of 5 mm after initiation of the cut. The vibrator and accelerometer were not mounted on the field instrument.

The tip of the blade extended about 5 mm beyond the surface of the leaf. Differences between blades, and any wear of the blade (we switched blades after cutting an average of 30 cm), were compensated for by normalizing the data according to values obtained cutting paper standards, although this turned out not to be necessary because the forces to cut the standards varied little (SD=6% of mean). For measurements of the less stiff blackberry leaves used for the laboratory colony, a notch was cut into the leaf to prevent bunching at the initiation of the cut.

#### Electron microscopy

For scanning microscopy, uncoated air-dried specimens were examined using a field emission scanning electron microscope (Amray 3300FE). For transmission electron microscopy, specimens were embedded in L. R. White resin, sectioned, and examined using a Philips CM12 transmission electron microscope operated at 80 kV.

## Results

### Cutting rate prediction

In order to test if the cutting rate is affected by the force required to cut a leaf, as measured by our apparatus, and to begin to build a model of the time and energy costs of cutting, we attempted to predict the averages and trends for cutting rates of the wild colony we studied in Panama from ant size and the force required to cut the leaves with a scalpel and the cutting rates of laboratory ants.

We used the principle that the maximum steady-state cutting rate is set by the maximum power available for cutting, divided by the energy used per meter of cut. We hypothesized that ants tend to cut at this maximum steady-state rate, or a constant fraction thereof, and that the power available for cutting is, like the volume for storing and converting energy, proportional to the body mass of the ant. If these assumptions are correct, the cutting rate should be

proportional to the mass of the ant divided by the force required to cut the leaf. Using the reported allometric relationship between head width and mass for *A. cephalotes* [mass is proportional to head width to the 2.5 power (Wetterer 1991)] and fitting the constant of proportionality to our cutting rate data for the laboratory colony, we arrived at the following model:

$$R_{\text{off-vein}} \cong 6.0 \times 10^{-4} H^{2.5} / F_{\text{scalpel}}, \quad (6)$$

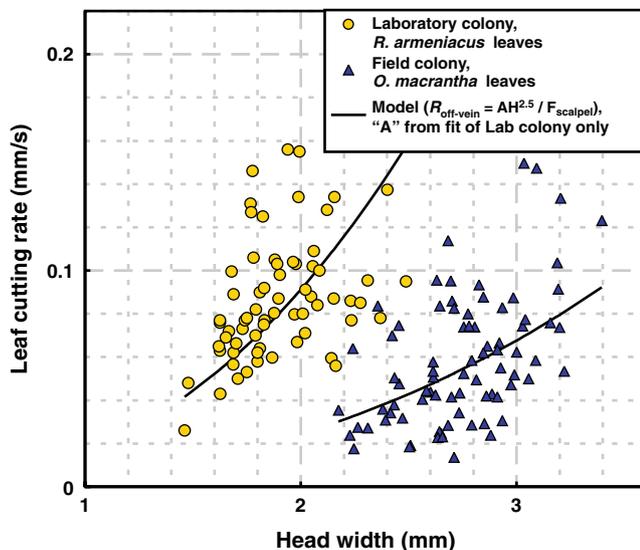
where the force to cut with a No. 11 surgical blade,  $F_{\text{scalpel}}$ , is in newtons, the head width,  $H$ , is in millimeters, and the cutting rate,  $R_{\text{off-vein}}$ , is in millimeters per second.

Figure 4 shows the laboratory and field colony data along with the cutting rate given by Eq. 6. The average ratio of predicted (using the constant from the fit of laboratory data only) to actual cutting rates for the field data was  $1.06 \pm 0.47$ .

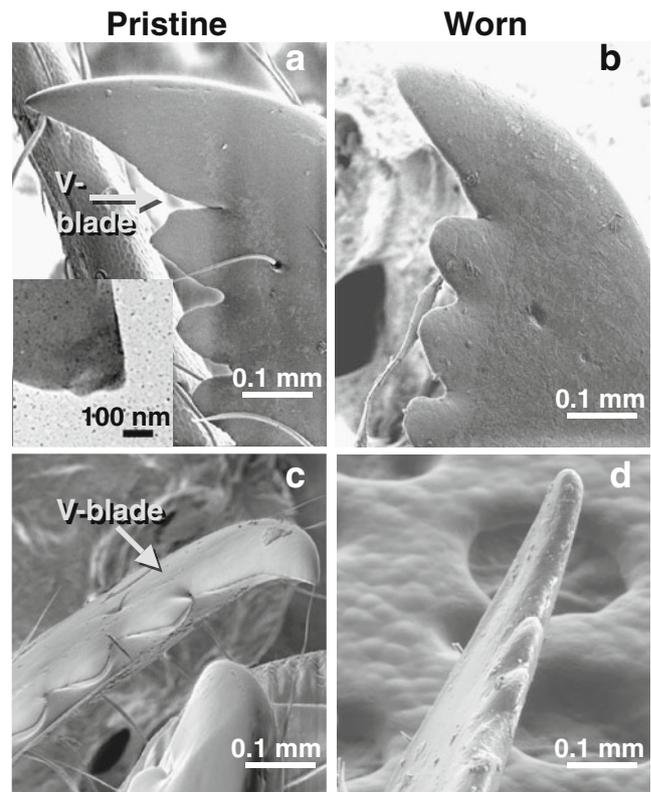
The success of this model supports the hypothesis that the cutting rate is inversely proportional to the force we measured, even though ants may be inefficient and may spend much more energy cutting than is required.

#### Cutting surfaces and wear

The model of Eq. 6 and Fig. 4 does not include wear. Wear is likely needed for an understanding of the productivity differences between individual ants: Fig. 5 shows great differences between pristine and highly worn mandibles. While the pristine blade edge radius was about 50 nm, the



**Fig. 4** The average cutting rates of the field and laboratory colonies are consistent with a model using ant size, the force to cut leaves with a scalpel, and a constant, fit only to the laboratory colony data. At any head width, the line for laboratory data is 3.71 times higher than the line for field data because this was the ratio of forces to cut the different leaf types



**Fig. 5** Pristine and highly worn mandibles of *A. cephalotes*, in face views (a, b) and cutting edge views (c, d). **a** The mandible of a 770-h-old ant isolated from the laboratory colony to prevent cutting. Projections of the first and second teeth together form a “V-blade” in the gap between these teeth (previously unreported to our knowledge) that may aid off-vein cutting by causing the leaf to self-align and by filling the gap between teeth with a blade. We have also observed V-blades in young adult *A. sexdens*. The inset transmission electron microscope image of a cross-section of the blade on the second tooth indicates that the blade radius is about 50 nm, about the sharpness of a new razor blade. Images of two other pristine blades confirmed this finding. **b** The mandible of a forager from the field colony with near-average head width (2.7 mm) and high wear of the second tooth (0.056 mm). The *O. macrantha* leaves were about 0.13 mm thick and so for this size of ant would have been cut mainly by the worn V-blade. **c** A late-stage pupa from the laboratory colony—the crack between the second and third teeth was probably due to drying after dissection. **d** A smaller ( $H=2.5$ ) forager from the field colony with high wear of the second tooth (0.050 mm) and a 17- $\mu\text{m}$  radius of the cutting edge of the first tooth

radius of a cutter’s blade with high wear was about 17  $\mu\text{m}$ , 340 times duller. Two examples of laboratory ants cutting with highly worn mandibles are shown in “Electronic supplementary material”, movie 3: [http://www.youtube.com/watch?v=gX\\_80kxF1Yk](http://www.youtube.com/watch?v=gX_80kxF1Yk). Both ants appear to have difficulties cutting and often make failed attempts to anchor cuts with their blunted leading mandible.

It is noteworthy that even a cutter showing relatively little wear (lower 20th percentile of cutters) had a 6- $\mu\text{m}$  blade edge. The large blade radii among the least worn mandibles of foragers may indicate that the blades are already worn from

leaf disk processing inside the nest (Hölldobler and Wilson 2009), before the foragers even leave the nest.

The required work to cut increases with mandible wear

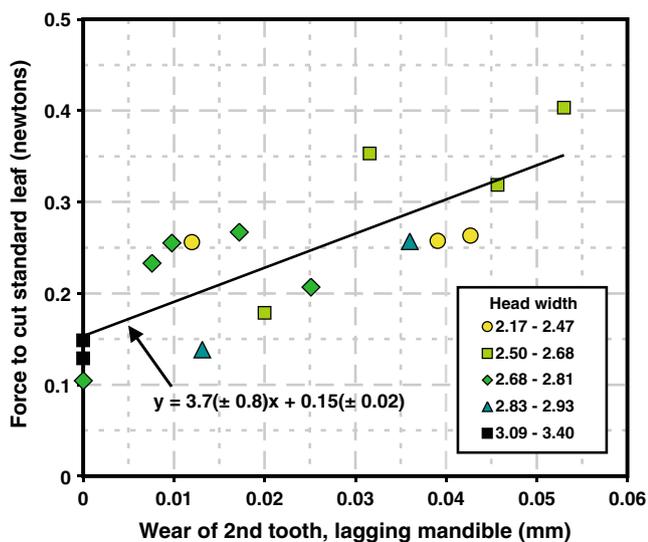
We studied the effects of wear by measuring the force required to cut a standard leaf with individual dissected mandibles from wild colony cutters. Figure 6 shows that the distance-averaged force ( $F_{\text{ant}}$ ) required to cut our standard leaves can be modeled as:

$$F_{\text{ant}} = (3.73 \pm 0.78)W_{\text{lagging}} + (0.153 \pm 0.022), \quad (7)$$

where  $W_{\text{lagging}}$  is a wear figure of merit based on the difference between the length of the second tooth on the lagging mandible and an estimate of its original length based on pupal measurements. There is a strong correlation between the required cutting force and tooth wear (Pearson's correlation,  $n=16$ ,  $r=0.79$ ,  $p=0.0003$ ).

The fit of data in Fig. 6, along with the distribution of wear in the collected ants, suggests that, compared to ants with pristine mandibles, cutting foragers with average wear of the second tooth on the lagging mandible ( $W_{\text{lagging}}=0.030$  mm) would require  $1.7 \pm 0.2$  times as much energy (force multiplied by distance) and for median wear of the most worn tenth ( $W_{\text{lagging}}=0.057$  mm) would require  $2.4 \pm 0.3$  times as much energy per cut.

The data in Fig. 6 were taken without vibrating the mandible to imitate the effects of stridulation (Tautz, Roces



**Fig. 6** The distance-averaged force (work/distance) required to cut standard leaves with dissected mandibles correlates with mandible wear (Pearson's correlation,  $n=16$ ,  $r=0.79$ ,  $p=0.0003$ ). Each point represents an average for four 3-mm cuts. Zero-wear mandibles were from isolated laboratory ants; other mandibles were from field colony cutters. Colors and symbols indicate the ant's head width—larger mandibles do not appear to require more work (Pearson's correlation,  $n=16$ ,  $r=0.15$ ,  $p=0.57$ ). The average force for scalpels was 0.16 N, slightly greater than for pristine mandibles

and Hölldobler 1995). We did not expect that vibrations would reduce the average required force because Tautz et al. did not report that the required force was reduced, only that it became more uniform and, even then, only for less “tough” leaves (likely much less “tough” than ours). Nevertheless, to test this possibility, the testing apparatus was equipped with a vibrator and accelerometer to replicate the reported vibrations associated with stridulation. Tests using both a worn and a pristine mandible did not show a force reduction for such vibrations (for the pristine mandible: vibration,  $3.20 \pm 0.91 \times 10^{-4}$  joules/3 mm; no vibration,  $3.20 \pm 0.77 \times 10^{-4}$  joules/3 mm; the difference was found to be less than 16% at a 95% confidence level [paired Student  $t$ -test,  $n=8$  pairs, hypothesized difference of means  $5.12 \times 10^{-5}$  joules/3 mm,  $t=1.89$ ,  $p=0.05$ ]).

#### Power output

An estimate of the power required to cut at the measured rate was made for each specific field colony ant and leaf, based on the wear of the second tooth, lagging mandible, the regression equation in Fig. 6, and the ratio of forces to scalpel-cut the standard leaf and the particular leaf that the ant was cutting. This estimate yielded an average required power of 11  $\mu\text{W}$  (for a mean head width of 2.71 mm and body mass of about 15 mg), with a strong dependence on head width.

The metabolic rate of 15 mg *Atta sexdens* individuals that were cutting Parafilm has been reported to be about 600  $\mu\text{W}$  (Roces and Lighton 1995). To test that Parafilm is a good substitute for leaves, we compared the force required to cut Parafilm (PM-992, [www.parafilm.com](http://www.parafilm.com)) using a No. 11 scalpel to that required to cut the leaves used in our study—Parafilm, 0.20 N; *P. lusitanica*, 0.16 N; *O. macrantha*, 0.14 N; *R. armeniacus*, 0.037 N. Using the 600- $\mu\text{W}$  metabolic rate, the estimated cutting efficiency was about 2% (we do not scale according to the force difference because, in our simple model, if the force is 1/2 as large, the cutting rate doubles and the energy consumption rate remains the same). While this 2% cutting efficiency is low (and may thus suggest a possible discrepancy between the force and the metabolic measurements), it does overlap with the range of efficiency for insect flight muscles, which is reported to be 2–34% (Josephson, Malamud and Stokes 2001).

#### Wear reduces cutting rate

A blind analysis scheme was used to test the hypothesis that wear reduces cutting rate. We used pre-selected multiple linear regression models to fit the wild colony data because we noted an inverse correlation between head width and tooth wear that would bias a simple correlation test. The results for the multiple linear regressions are given in

Table 1 with the data and fits plotted in Fig. 7. Correlations between cutting rate and other variables are given in Tables 2 and 3; only correlations with wear and head width were significant.

For off-vein cutting, the pre-selected multiple linear regression model yielded the following equation:

$$R_{\text{off-vein}} = (-0.174 + 0.087H) + (2.9 - 1.16H)W_{\text{off-vein}}, \tag{8}$$

where  $R_{\text{off-vein}}$  is the off-vein cutting rate in millimeters per second,  $H$  is the head width in millimeters, and  $W_{\text{off-vein}}$  is the tooth length-based wear figure of merit for off-vein cutting as described in the “Materials and methods” section.

Table 1 shows that, for this model, the probability that the slopes of lines giving cutting rate as a function of wear (Fig. 7) are less than zero is greater than 95% for head widths greater than 3.0 mm. For example, an ant with a head width of 3.1 mm and the median level of wear of the 10% of ants with the most wear ( $W_{\text{off-vein}}=0.05$ ), the cutting rate given by the regression is 62% ( $\pm 22\%$ ) of the rate given for the same size of ant with zero wear.

For vein cutting, cutting rates varied by a factor of 30, so we pre-selected a different multiple linear regression model that yielded the following equation for cutting rate:

$$\ln(1 \times 10^6 R_{\text{vein}}) = 3.3 + 1.51H - 25W_{\text{vein}}, \tag{9}$$

where  $W_{\text{vein}}$  is the wear figure of merit for vein cutting.

The standard deviations given in Table 1 indicate that, for this model, the probability that the slopes of the lines giving cutting rate from wear (Fig. 7) were less than zero was 96.1%. Ants with high mandible wear ( $W_{\text{vein}}=0.05$ ) are predicted by the regression to cut veins 28% (one sigma band, 14% to 58%) as fast as ants with zero wear, independent of size.

Foragers with the most worn mandibles carry instead of cut

Wear may affect task selection as well as cutting rate and energy cost. Figure 8 shows the distribution of wear for

equal and size-balanced samples of field colony ants that were cutting leaves in, and carrying leaf disks away from, our artificial tree. The distributions of cutters and carriers with greater than median wear differed significantly (Wilcoxon two-sample test,  $n=22$ ,  $p=0.01$ ). Of the tenth of the ants with the most worn mandibles, eight of nine were carrying (binomial test,  $n=9$ ,  $p=0.02$ ). According to the fit in Fig. 6, this most worn tenth would have required an average of 2.7 times as much energy to cut our standard leaf than if their mandibles had been pristine.

### Discussion

#### Constant power model

The cutting rate reductions and the increases in cutting energy that we found were consistent with being reciprocals of each other. For example, for a 3.1-mm head width ant with the median wear level of the most worn 10% of cutters, we found that wear increased the energy required per off-vein cut by a factor of  $2.4 \pm 0.3$  and reduced the off-vein cutting rate by a factor of  $0.62 \pm 0.22$ . Thus, our observations are consistent with our model in which the cutting power is constant and the ant cuts at twice the rate when half the force is required. We therefore include wear in the constant power model of Eq. 6, again assuming that cutting rate is proportional to the ratio of ant mass to cutting force and assuming that the cutting force, given by Eq. 7 for standard leaves, scales for other leaves according to the ratio of required scalpel forces ( $F_{\text{scalpel}}/0.16$ ) and assuming that the average wear of 0.030 mm gives the constant of Eq. 6:

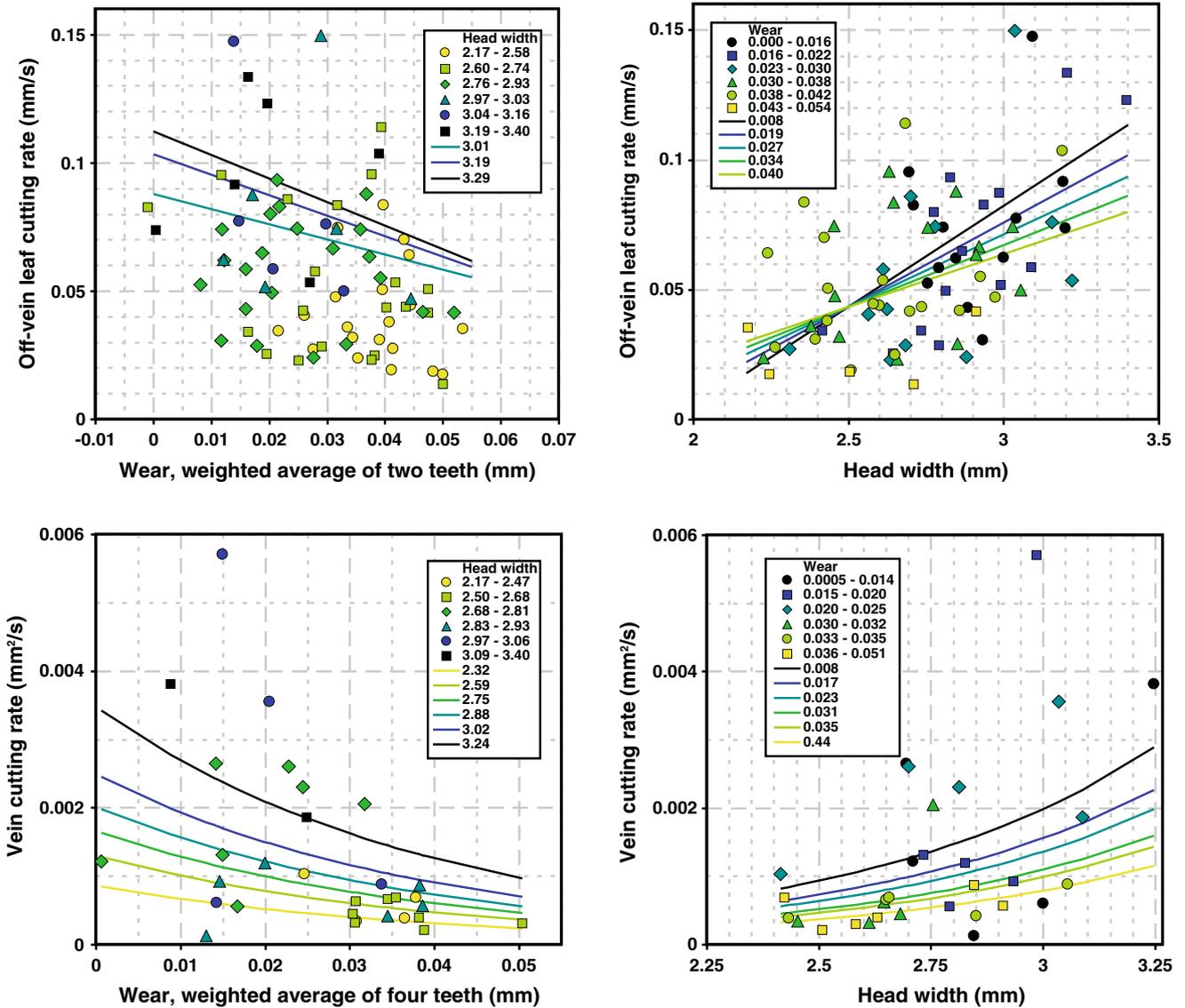
$$R_{\text{off-vein}} \cong \frac{4.26 \times 10^{-5} H^{2.5}}{F_{\text{scalpel}}(W_{\text{lagging}} + 4.10 \times 10^{-2})}, \tag{10}$$

where  $R_{\text{off-vein}}$  is the off-vein cutting rate in millimeters per second,  $H$  is the head width in millimeters,  $F_{\text{scalpel}}$  is the force to cut the leaf with a No. 11 surgical blade, in newtons, and  $W_{\text{lagging}}$  is the wear figure of merit for the lagging

**Table 1** Coefficients,  $R^2$  values, slopes, and regions of significance for multiple linear regression fits of the cutting rate data ( $\pm$  values are standard deviations)

Predicted cutting rate (R)	Coefficients				$R^2$	Slope (region of significance <sup>a</sup> , $p < 0.05$ )	
	Constant	Of head width (H), mm	Of wear (W), mm	Of WH		$\Delta R / \Delta W$	$\Delta R / \Delta H$
Off-vein cutting rate, mm/s	$-0.174 \pm 0.091$	$+0.087 \pm 0.032$	$+2.9 \pm 2.6$	$-1.16 \pm 0.94$	0.29	$0.087 - 1.16W_{\text{off-vein}}$ ( $W_{\text{off-vein}} < 0.055$ )	$2.9 - 1.16H$ ( $3.0 < H < 3.40$ )
$\ln(\text{vein cutting rate} \times 1 \times 10^6)$ , $\text{mm}^2/\text{s}$	$+3.3 \pm 2.2$	$+1.51 \pm 0.74$	$-25 \pm 14$	0	0.33	$1.51 \pm 0.74$	$-25 \pm 14$

<sup>a</sup> When the slope depends on wear (W) or head width (H), the range of values over which the 95% confidence interval does not include zero slope is included in parentheses



**Fig. 7** Data and multiple linear regression fits for off-vein (*top plots*) and vein (*bottom plots*) cutting. Value ranges for the third dimension of each plot are indicated by *symbols* and *colors*. The regression line

for a central value from each of these color bins is plotted in the same color as long as the 95% confidence interval does not include zero slope

**Table 2** Correlation (Spearman’s rank) between off-vein cutting rate and other variables

Variable	Mean ± SD	$r_s$ values	Two-sided $p$ -values	$n$ , number of samples <sup>a</sup>
Head width (mm)	2.74±0.27	0.48	<0.0001	79
Number of ants on leaf	16±10	0.21	0.33	23
Force to cut leaf with scalpel (newtons)	0.139±0.038	0.25	0.23	25
Temperature (°C)	23.2±1.2	0.22	0.079	65
Time (hours after midnight, local standard)	2.7±1.3	−0.22	0.056	79
Wear (normalized mm)	0.030±0.013	−0.35	0.0016	79

<sup>a</sup> Multiple ants could be collected for a single leaf. For this reason, the number of leaves, instead of the number of ants, was used as a conservative “ $n$ ” in determining the  $p$ -values for the “force to cut leaf” and “number of ants on leaf” variables. The average cutting rate for all ants collected from a leaf was used in the correlation with cutting rate for these two variables. Otherwise, the “ $n$ ”s represent the number of ants sampled

**Table 3** Correlation (Spearman's rank) between vein cutting rate and other variables

Variable	Mean $\pm$ SD	$r_s$ values	Two-sided $p$ -values	$n$ , number of samples <sup>a</sup>
Head width (mm)	2.76 $\pm$ 0.21	0.47	0.0079	31
Number of ants on leaf	15.1 $\pm$ 8.0	-0.21	0.41	17
Temperature ( $^{\circ}$ C)	23.4 $\pm$ 1.3	-0.12	0.57	26
Time (hours after midnight, local standard)	2.5 $\pm$ 1.5	-0.056	0.77	31
Wear (normalized, mm)	0.026 $\pm$ 0.011	-0.51	0.0039	31

<sup>a</sup> Multiple ants could be collected for a single leaf. For this reason, the number of leaves, instead of the number of ants, was used as a conservative “ $n$ ” in determining the  $p$ -values for the “number of ants on leaf” variable. The average cutting rate for all ants collected from a leaf was used in the correlation with cutting rate for this variable. Otherwise, the “ $n$ ”s represent the number of ants sampled

mandible, equal to the difference between the pupal length of the second tooth and the length at the time of cutting, in millimeters.

While Eq. 10 does not predict the cutting rate as accurately as Eq. 8 for the particular conditions of the regression, it is based on a physical model that can be generalized. Equation 10 accounts for 39% of the variance ( $R=0.62$ ) in the cutting rate for the full sampled range of cutter head widths (1.87–3.65 mm) for the field colony.

#### Effects of wear on the rate of energy collection

Which is the more deleterious effect of wear, the reduction in cutting rate or the increase in cutting energy? To investigate, we assumed that the relevant energy quantity relating leaf cutting to the fitness of an individual cutting ant is the energy flow from the leaf material cut by that ant to the reproductive brood  $P_{\text{repro}}$  (watts), and we modeled this as:

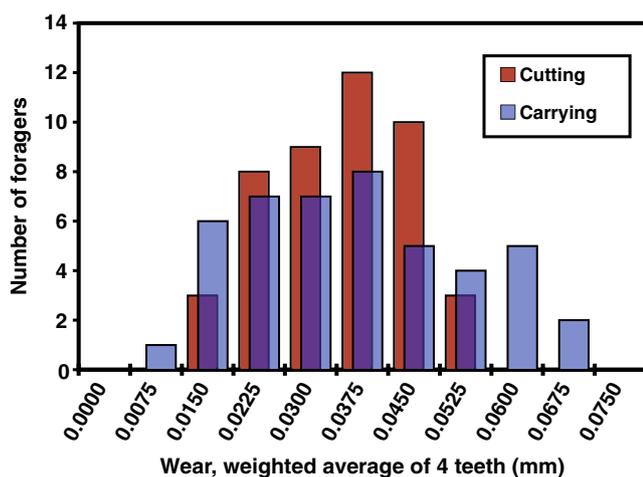
$$P_{\text{repro}} = M_{\text{rate}}(U_{\text{leaf}} - U_{\text{cut}} - U_{\text{process}}) - P_{\text{non-repro}}, \quad (11)$$

where  $M_{\text{rate}}$  is the rate at which the ant cuts leaf mass into disks for transport (kg/s),  $U_{\text{leaf}}$  is the caloric density

of the leaves (joules/kg),  $U_{\text{cut}}$  is the energy used by the ant to cut a kilogram of leaves into transportable disks,  $U_{\text{process}}$  is the additional energy required directly for processing, including transport and conversion to fungus within the nest, and  $P_{\text{non-repro}}$  is the power flowing from the leaf material cut by the ant to non-reproductive ants for everything but the direct cutting, carrying, and processing of that specific material.

The cutting rate reduction has a simple effect on the energy flow: if  $M_{\text{rate}}$  is halved, the energy flow is halved. The effect of an increase in cutting energy is less straightforward. Typical energy densities for leaves are about  $1 \times 10^6$  J/kg, while we estimated that the energy for cutting the field colony leaves with pristine mandibles was almost two orders of magnitude lower, about  $1.3 \times 10^4$  J/kg [assuming a 600- $\mu$ W cutting metabolic rate (Roces and Lighton 1995)]. Thus, the cutting energy has a small fractional effect on energy flow, and the time cost is greater than the energy cost, unless most of the energy from a leaf disk is used in processing that leaf disk.

If most of the leaf energy were used in processing, then ants with the most worn mandibles might not cut because the cutting and processing energy together exceeded the energy in the leaf disk. Assuming that this break-even point is at 2.5 times the pristine mandible cutting energy, we estimate that the processing cost,  $U_{\text{process}}$ , would have to be about 30 times greater than the cutting cost, and, as a result, the “profit margin” (the fraction of leaf calories not used in cutting and processing) would be about 2% for cutting with pristine mandibles. While we do not have metabolic rate data for in-nest processing, a cost 30 times greater than for the original cut may not be unreasonable since the leaf disks are cut into much smaller pieces within the nest. If profit margins were just a few percent, an extra 50 m of transport could make harvesting unprofitable and so we would expect that the farthest harvesting sites from the nest would have the highest ratio of leaf energy density,  $U_{\text{leaf}}$ , to cutting energy density,  $U_{\text{cut}}$ . Low profit margins might also help explain the nearly negligible reduction of forest foliage on large scales from leaf-cutter



**Fig. 8** Foragers with the most worn mandibles tend to carry instead of cut (binomial test for the 10% with the highest wear,  $n=9$ ,  $p=0.02$ ). The two sample sets contain equal numbers and are matched by head width

activity (Wirth, Herz, Ryel, Beyschlag and Hölldobler 2003).

#### Costs of wear for the colony

Our results suggest that wear nearly doubled the time and energy costs of leaf cutting for the field colony even though the ants with the most worn mandibles did not cut. Based on the distribution of wear in the collected cutters, the distances they cut, and the effect of wear on force and cutting rate (Eqs. 7 and 10), we estimate that, if the field colony cutters all had pristine mandibles, the colony would have spent a factor of 0.58 as much energy and time making the observed off-vein cuts. For vein cuts, the factor was estimated to be 0.49, using Eq. 9. Combined according to the fraction of time spent on each, our estimate is that a hypothetical colony with only pristine mandibles would have spent 0.56 as much time and energy cutting leaves outside the nest than our field colony.

In addition to increasing the costs of cutting outside of the nest, wear must also increase the cost of cutting up the leaf disks within the nest, but quantifying this cost, as well as determining how well our single observation generalizes to other colonies, awaits further research.

#### Task allocation and partitioning

The observation that the ants with the most worn mandibles carried but did not cut suggests a form of ability-based task partitioning that has not been previously reported. Published examples of ability-based task partitioning have been associated with time-invariant, genetically determined traits such as ant size or stimulus sensitivity in bees (Gordon 1996; Ratnieks and Anderson 1999; Anderson and Ratnieks 2000; Hart, Anderson and Ratnieks 2002). In the present instance, ability level (cutting efficiency) and task selection vary in time as mandibles wear.

#### *Wear or aging?*

The selection of carrying over cutting may be prompted by advanced age, independent of wear, or it may be prompted by a reduction in cutting efficiency that is evaluated and used in task selection by the individual ant. The latter possibility would be similar to the apparent self-evaluation in the acceleration of the temporal sequence of tasks observed in ants and bees that have been artificially injured to shorten life expectancies (Moron, Witek and Woyciechowski 2007; Woyciechowski and Moron 2009). We hypothesize that ants self-evaluate their cutting ability and stop cutting if the cut is not progressing efficiently and either find a new place to initiate a cut or carry instead. Studies of task selection with ants that have artificially worn mandibles and ants that have

been prevented from using their mandibles to maintain sharpness would discriminate between the age and the self-evaluation hypotheses. Whether the change in behavior is prompted by age or by self-evaluation, the ultimate cause is likely to be the great reduction in cutting efficiency associated with worn mandibles.

#### *Task partitioning was sub-optimal*

We compared the actual division of labor into cutters and carriers to an estimate of the optimal division of labor, made using cutting rate estimates (Eq. 10) and estimates of laden and unladen walking rates from Burd (1996). We assumed a pool of foragers made by weighting our cutting and carrying samples by the estimated fraction of time spent on each task for our 85-m foraging trail. These ants were then ordered according to the ratio of estimated cutting rate to the estimated average walking rate for an out-and-back trip retrieving a 15-mg leaf disk. The ant at the top of the list, the most efficient ant at cutting relative to carrying (where time, not energy is the figure of merit), was assigned to be a cutter, while the number of ants needed to carry this ant's cut disks were assigned from the relatively efficient carriers at the bottom of the list. This process was repeated until all ants had been assigned tasks. Cutters were assumed to stay out for 2 h and to carry a disk when returning to the nest. For this attempt at an optimized assignment of tasks, the foraging rate was estimated to be 4.0  $\mu\text{g}$  of leaf material per working ant per second, 11% greater than for random task allocation. For the actual allocation sampled in the field, the foraging rate was estimated to be only 1.4% greater than for a random task allocation (the difference with random allocation was significant: ten different distributions of cutters and carriers were compared to 15 different distributions in which ants were randomly assigned to be cutters or carriers; Student's *t*-test,  $n=10$ ,  $15$ ,  $t=3.27$ ,  $p=0.003$ ). This estimate of optimal task allocation is imperfect because of the imperfect cutting rate prediction ( $R=0.62$ ). We estimated the increase in foraging rate that would result from task optimization based on perfect prediction of cutting rate using a model in which additional variables or measurement uncertainties accounted for the imperfect prediction by causing normally distributed deviations around the prediction. For this model, the optimal rate obtained with perfect prediction of cutting rate was 14% greater than for random task allocation (instead of 11%), and the actual rate was 1.9% greater than for random task allocation (instead of 1.4%).

Thus, the partitioning of labor into cutters and carriers appeared to be sub-optimal but superior to random for foraging from our artificial tree. Sub-optimal task allocation has been reported in bees (Arathi, Ho and Spivak 2006) and ants (Burd and Howard 2005). A sub-optimal, though better

than random, task allocation could result from ants attempting to start a cut but abandoning it and switching to carrying if their cutting rate was too low or from increasing tendency to carry with age.

## Conclusion

Since typical levels of wear are associated with, approximately, a doubling in required energy for cutting, compounded by a doubling in cutting time, we would expect wear to produce a strong selection pressure. This pressure may promote preference for less abrasive leaves with high ratios of caloric content to cutting energy; it may promote wear-resistant mandible composition and structure; it may promote steady, wear-reducing cutting techniques over chopping; and it may help account for the much shorter lifespan of workers relative to queens. In addition to avoiding cutting with worn mandibles, tasks may be partitioned to avoid unnecessarily damaging sharp mandibles with such tasks as trail debris removal. We have previously suggested that such wear avoidance is a reason that young adults do not cut inside the nest before their teeth are hardened by zinc (Schofield, Nesson and Richardson 2002). Task partitioning to avoid the use of undeveloped, worn, or damaged mandibles is likely one of the advantages of eusociality and may lead to longer average lifespans in social insects than in their solitary relatives. Wear's strong effect on leaf-cutter performance supports the hypothesis that small "tools" are particularly susceptible and that wear and its avoidance are important in the behavioral ecology and energetics of many other small organisms.

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**Ethical standards** The experiments described in this paper complied with the current laws of the Republic of Panama and of the United States of America.

**Conflicts of interest** The authors declare that they have no conflicts of interest.

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