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## The effect of load length, width and mass on transport rate in the grass-cutting ant *Atta vollenweideri*

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**Abstract** In the present study we investigated the economics of load transport in the grass-cutting ant *Atta vollenweideri* by focusing on the effects of load mass, width and length on individual transport rates. Both running speed of foragers and the amount of material transported a given distance per unit time, i.e. gross material transport rate, were evaluated in both field and laboratory colonies. In order to separate the effects of load mass, load length and width on transport rate, workers were presented with paper fragments which differed twofold either in length, width or mass, but not in the other parameters. When controlling for fragment mass, both running speed of foragers and gross material transport rate were observed to be higher when they carried short fragments: A twofold increase in fragment length had a marked negative effect on manoeuvrability during transport and, as a consequence, on material transport rate. In contrast, if fragment mass was doubled and length maintained, running speed differed according to the mass of the loads, with heavier fragments being transported at the slower pace. For the sizes tested, heavy fragments yielded a higher transport rate in spite of the slower speed of transport, as they did not slow down foragers so much that it counterbalanced the positive effects of fragment mass on material transport rate. Doubling the width of the fragments without changing their mass had no influence on running speed and transport rate. When presented with a choice of dropped fragments differing in the size variables mentioned above, workers discriminated among fragments of different size and preferred shorter fragments, thus rejecting loads that are associated with higher travel times and lower material transport rates. It is argued that, based on the energetics of cutting, workers might maximize their individual harvesting rate by cutting long grass fragments, since the longer a grass

fragment, the larger the amount of material harvested per unit cutting effort. Our results indicate, however, that larger loads negatively affect transport rates. The sizes of the fragments cut by grass-cutting ants under natural conditions may represent the outcome of an evolutionary trade-off between maximizing harvesting rate at the cutting site and minimizing the effects of fragment size on material transport rates.

**Keywords** Load size · Foraging · Transport · Decision-making · Running speed

### Introduction

Leaf-cutting ants with their conspicuous trunk trails are a common sight in many tropical and subtropical regions of the New World. Foragers travel 100 m or more to established patches, where plant material is cut and transported to the nest. In the nest, leaf fragments are processed by gardening workers to serve as substrate for a symbiotic fungus (Weber 1972). On long foraging trails, a roundtrip to the patch by a single forager can take several hours. Since the carried fragments can be several times heavier than the workers that carry them, thus affecting transport speed, the fragment sizes cut by the ants are expected to have important effects on material transport rate (Lighton et al. 1987; Rudolph and Loudon 1986; Wetterer 1990, 1994). Consequently, it is likely that fragment-size determination by foraging workers represents the outcome of an evolutionary trade-off among constraints resulting from the energetics of both cutting behaviour and transport.

To date, most investigations on leaf-cutting ant foraging behaviour refer to those species which harvest dicotyledonous leaves, such as *Atta cephalotes*, *A. colombica* and *A. sexdens*. To cut a leaf fragment, workers of these species anchor their hind legs at the leaf edge and rotate around their body axis, so that fragments have a roughly semicircular shape. As a consequence, fragment size correlates with ant body size and is limited by the

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maximal reach of the ant while cutting (Lutz 1929). Yet, workers are able to alter their reach while cutting in order to cut smaller leaf fragments. It has been observed that the size of the fragment cut depends on leaf area density (leaf mass per surface area), i.e. the “denser” a leaf, the smaller the fragments (Cherrett 1972; Roces and Hölldobler 1994; Rudolph and Loudon 1986). In addition, the motivation of workers to return to the nest influences leaf fragment size: at the initial phase of a foraging process, or upon discovery of a highly attractive source, workers were observed to cut smaller leaf fragments (Roces and Núñez 1993; Roces and Hölldobler 1994) than after a foraging column had been established. Such differences in load-size determination have a number of consequences on foraging performance: regarding cutting, cutting length and therefore cutting time decreases with decreasing fragment size, so that ants cutting smaller fragments spend less time at the source and run faster on the trail because of their lighter loads, so as to return sooner to the colony in order to recruit nestmates.

Regarding the effects of fragment size on transport, travel speed declines with increasing load mass, so that travel time per roundtrip increases (Burd 1996, 2000; Lighton et al. 1987; Rudolph and Loudon 1986). In spite of their slower speed when carrying larger fragments, workers may achieve higher material transport rates owing to the larger loads they carry. But longer travel times, with the concomitant reduction in roundtrip frequency, may negatively affect the probability of information transfer and therefore the intensity of recruitment (Roces and Hölldobler 1994; Roces and Núñez 1993). Furthermore, longer travel times might result in a longer exposure to predators and parasites (Feener 1990), thus increasing foraging risks.

While variation in leaf fragment size is necessarily associated with different cutting effort in leaf-cutting ant species harvesting semicircular fragments, the situation is rather different for grass-cutting ants. Workers of the subtropical species *Atta vollenweideri* harvest mainly grasses (Jonkman 1976, 1979; Robinson and Fowler 1982). During foraging, workers climb on a grass blade and cut across its width, which results in the selection of a longish, more or less rectangular grass fragment. Therefore, cutting length is represented by grass width, which usually does not differ very much along the blade except at its tip. Hence, cutting a larger (longer) fragment neither implies a higher cutting effort nor a longer cutting time, if grass toughness remains unchanged along the blade. Workers may therefore harvest more material per unit cutting effort by simply cutting very long fragments. As a consequence, selection of very long fragments would be expected if only the energy investment during cutting is considered. But since fragments are transported to the nest, fragment length may have substantial effects on manoeuvrability and speed of transport, factors that are expected to set an upper limit to the fragment size selected by workers during harvesting.

In *A. vollenweideri*, fragment length was observed to average 43 mm (Daguerré 1945), being therefore much

longer than the ant body length. During transport, a worker takes a fragment with its mandibles at one end and carries it in a more or less vertical position, usually inclined backward forming an angle of between 45° and 90° with the ant body axis. Manoeuvrability during transport of very long fragments and therefore walking speed might be particularly affected, because of the marked displacement of the center of gravity. Furthermore, workers carrying longer fragments might be more likely to be hindered by obstacles on their way to the nest. Thus, fragment length is expected to influence running speed, and therefore material transport rates.

In the present study, we investigated the economics of load transport in the grass-cutting ant *A. vollenweideri* by focusing on the effects of load size (mass, length and width) on gross material transport rate to the nest. We first measured the length of natural grass fragments cut by workers in field colonies. We then presented workers of both field and laboratory colonies with artificial fragments made of paper, in the size range observed for natural grass fragments. Fragments differed twofold either in length but not in mass, or in mass but not in length, or in both variables, so as to assess separately the effects of each of these variables on running speed and material transport rate of laden workers. Additionally, the effects of fragment width were evaluated. Finally, workers from a field colony were presented with a choice between fragments differing in the variables mentioned above, in order to investigate whether workers are able to discriminate between the different size parameters when collecting dropped fragments prior to their transport to the nest.

## Materials and methods

### Length of plant fragments cut by the ants in the field

All field experiments were carried out on a mature colony of *A. vollenweideri* in the El Bagual Biological Station in Formosa, north Argentina, from October to December 1999. In order to quantify the fragment sizes harvested naturally by the ants, we collected randomly during four consecutive days 33 foragers with their loads shortly after they had finished cutting their fragments out of the sedge *Cyperus entrerrianus* (Cyperaceae). The natural trail was 10 m long and further experiments were performed on it. Ant and fragment masses were determined to the nearest 0.1 mg, and fragment length and width were measured to the nearest 0.5 mm.

### Effects of load length

In order to separate the effects of load length and mass on running speed, workers were presented with three types of fragments that differed either in length or in mass, but not in the other parameter, width. The fragments were cut out of standard paper (80 g/m<sup>2</sup>), soaked with orange juice for at least 1 h, and then dried. Based on the measurements of the plant fragments naturally cut, we chose a fragment width of 4 mm and lengths of either 40 mm (henceforth: “long fragment”; mass range, 14–17 mg), or 20 mm (“short fragment”; mass range, 9–11 mg). The third fragment type was made by sticking two wet fragments together, forming a short “double fragment” of 20 mm in length and also 4 mm in width. Because these fragments had been stuck together, they were slightly, but not significantly, heavier than the long ones (mass range, 16–19 mg; *t*-test for independent samples,  $n_{(\text{double})}=61$ ,  $n_{(\text{long})}=64$ ,  $P>0.05$ ).

Fragments were placed on an active trail. We presented them alternating between the three types and measured the running speed of the first ten laden workers running back to the nest on a 50-cm trail sector. Laden foragers were then caught and weighed. The sample size ranged from 61 to 65. Gross transport rate per individual was calculated by multiplying running speed by the mass of the fragment. During measurements, the ambient temperature varied between 18.2°C and 24.5°C and humidity between 73% and 100%. The alternating presentation of fragments was chosen to control for differences in climate, time and overall foraging activity.

Similar experimental series were performed in the laboratory at the University of Würzburg in Germany. For these, workers from a laboratory colony of *A. vollenweideri* were allowed to forage in an arena of approximately 1×0.5 m connected to the nest by a 1.5-m-long wooden bridge. Fragments and the experimental procedure of the experiment were the same as in the field experiment, with the exception that a given fragment type was presented during an experimental day. The experiment was run at a temperature of 21–23°C and a humidity of 27–34%. Fragment mass ranged from 16 to 18 mg for the long, 15–17 mg for the double and 9–10 mg for the short fragments.

#### Effects of load width

The effects of load width on running speed, irrespective of load mass, were investigated in a field experiment in the same manner as described above, but using fragments that only differed in width. From the three fragment types described above, we used the heaviest, because an effect of width, if any, would be more likely to be detected in heavy fragments. Fragments were 40 mm long and had a width of either 4 mm or 2 mm, with the latter type being again a double fragment. Fragment mass did not differ statistically between the groups, and ranged from 15 to 17 mg (“wide fragments”), or 16–19 mg (“narrow fragments”). A total of 60 laden workers per fragment type were recorded. Gross transport rate per individual was calculated as indicated above.

#### Fragment-size preference

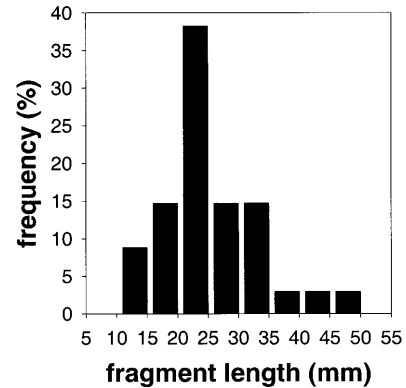
In order to investigate whether ants discriminate between fragments of different size when collecting fragments prior to transport to the nest, workers from a field colony were presented with a choice between the three different artificial fragments described above. Fragments ranged from 8 to 9 mg (short), 16–18 mg (double) and 16–18 mg (long). Ten fragments of each type were placed together on an active trail, forming a loose pile of 30 fragments. Care was taken so that fragments were not too crowded. The first ten workers collecting fragments were caught after they had left the pile walking towards the nest, and the fragment type chosen was noted. A total of 20 replicates were performed.

## Results

#### Lengths of grass fragments cut

The distribution of lengths of natural grass fragment cut by the ants in the field is shown in Fig. 1. Fragments ranged from 12 to 49 mm, with most fragments being 20–25 mm long (mean±SD, 25.4±7.9 mm;  $n=33$ ). The width of the fragments ranged from 2 to 8 mm, with most fragments being 3–5 mm wide (mean±SD, 4.4±1.8 mm). Load weight ranged from 3.1 to 53.4 mg (mean±SD, 18.9±10.8).

The body mass of workers carrying the grass fragments varied from 5.8 to 23.1 mg (average, 12.0±3.8 mg,  $n=33$ ).



**Fig. 1** Frequency distribution of lengths of grass fragments (*Cyperus enterrianus*) naturally cut by ants in the field ( $n=33$ ). Numbers on the x-axis indicate the upper limit of the respective range, with the limit being included

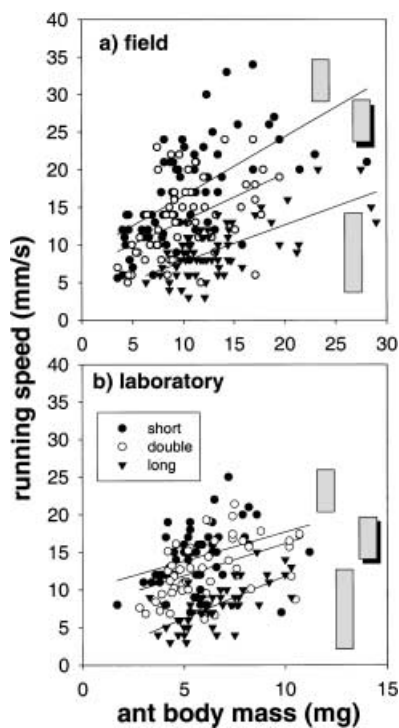
While fragment mass correlated significantly with ant mass ( $r^2=0.38$ ,  $P<0.005$ ), load length did not ( $r^2=0.14$ ,  $P=0.1$ ). This is probably due to the natural variation in fragment width, and the significant negative relationship between load width and length ( $r^2=0.27$ ,  $P<0.005$ ; data not shown). The topic of load-size determination and size matching between ant size and load size will be discussed in more detail in a future publication.

#### Effects of load length on both running speed and gross transport rate

For the three different fragment types, running speed of laden workers significantly correlated with ant mass. This was the case for both field and laboratory experiments (Fig. 2a, b). The three regression lines differ significantly from each other with the short (and lightest) fragments being carried fastest [analysis of covariance (ANCOVA) for short and double fragments, equal slopes but different intercepts: field,  $F_{(1,123)}=13.55$ ,  $P<0.005$ ; laboratory,  $F_{(1,102)}=6.86$ ,  $P<0.05$ ]. In the two fragments types with the same mass, the short fragments were carried significantly faster than the long ones [ANCOVA for double and long fragments, equal slopes but different intercepts: field,  $F_{(1,122)}=61.29$ ,  $P<0.0001$ ; laboratory,  $F_{(1,100)}=88.96$ ,  $P<0.0001$ ].

The differences in speed observed between the transportation of short and double fragments are much smaller than those between the transportation of long fragments and both short and double ones. Therefore, a two-fold increase in load length slowed down the running speed much more than a twofold increase in mass. For the same mass, longer fragments were carried at a slower speed. This was observed in both field and laboratory experiments.

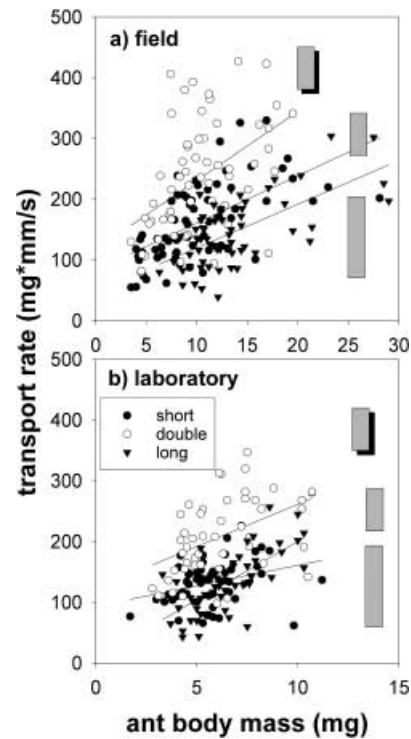
Using the data of running speed and load size, gross material transport rate per individual was calculated as the product between these two variables. This value may characterize more properly the foraging performance at



**Fig. 2a, b** Running speed of foragers carrying an orange-treated paper fragment. **a** Field colony: short fragments,  $y=8.54+0.79x$ ,  $r^2=0.36$ ,  $n=65$ ,  $P<0.0001$ ; double fragments,  $y=6.72+0.65x$ ,  $r^2=0.23$ ,  $n=61$ ,  $P<0.001$ ; long fragments,  $y=3.11+0.47x$ ,  $r^2=0.41$ ,  $n=64$ ,  $P<0.0001$ . **b** Laboratory colony: short fragments,  $y=10.18+0.74x$ ,  $r^2=0.09$ ,  $n=56$ ,  $P<0.05$ ; double fragments,  $y=7.56+0.86x$ ,  $r^2=0.22$ ,  $n=49$ ,  $P<0.001$ ; long fragments,  $y=0.49+1.14x$ ,  $r^2=0.47$ ,  $n=54$ ,  $P<0.0001$ . Note differences in scale on the x-axis between (a) and (b). The shaded boxes symbolise the three different fragment types used during the experiments

the colony level, since it represents a measure of the amount of material being transported to the colony over a given distance per unit time (Lutz 1929). The results of field and laboratory experiments are shown in Fig. 3a, b, respectively. For fragments having the same length but different mass (short and double type), transport rate was higher for the heavier than for the lighter ones [ANCOVA, equal slopes, different intercepts: field,  $F_{(1,123)}=33.88$ ,  $P<0.0001$ ; laboratory,  $F_{(1,102)}=59.09$ ,  $P<0.0001$ ]. This indicates that in the range tested, the increase in material transported achieved by taking the larger load exceeds the negative effects of mass on speed (see Fig. 2a). On the other hand, for fragments of the same mass but different length, transport rate was significantly lower for the long fragments [ANCOVA, equal slopes, different intercepts: field,  $F_{(1,122)}=89.77$ ,  $P<0.0001$ ; laboratory,  $F_{(1,100)}=75.88$ ,  $P<0.0001$ ], because of the slower running speed.

Ant body mass in this experiment ranged from 3.5 to 29.0 mg for the field colony and from 1.7 to 11.8 mg for the laboratory colony, so the laboratory colony had notably smaller foragers ( $t$ -test for independent samples:  $t=15.3$ ,  $df=468$ ,  $P<0.0001$ ).



**Fig. 3a, b** Gross transport rate of foragers carrying an orange-treated paper fragment. **a** Field colony: short fragments,  $y=83.69+7.75x$ ,  $r^2=0.36$ ,  $n=65$ ,  $P<0.0001$ ; double fragments,  $y=117.60+11.35x$ ,  $r^2=0.23$ ,  $n=61$ ,  $P<0.0001$ ; long fragments,  $y=47.85+7.21x$ ,  $r^2=0.41$ ,  $n=64$ ,  $P<0.0001$ . **b** Laboratory colony: short fragments,  $y=93.65+6.77x$ ,  $r^2=0.09$ ,  $n=56$ ,  $P<0.05$ ; double fragments,  $y=122.44+13.93x$ ,  $r^2=0.22$ ,  $n=49$ ,  $P<0.001$ ; long fragments,  $y=8.29+19.21x$ ,  $r^2=0.47$ ,  $n=54$ ,  $P<0.0001$ . Note differences in scale on the x-axis between (a) and (b). The shaded boxes symbolise the three different fragment types used during the experiments

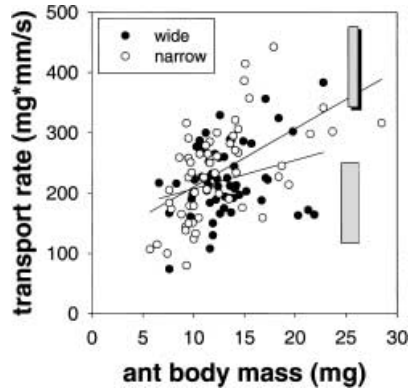
Effects of load width on both running speed and transport rate

Running speed and gross transport rates showed a significant correlation with ant body mass, which ranged from 5.7 to 28.5 mg (Fig. 4). Since the two fragment sizes used in the experiment differed in width but had the same mass, gross transport rates are obtained by multiplying speed values for both fragment types by the same mass value. As a consequence, only the curve for gross transport rate is plotted on Fig. 4. The regression lines for the transport speed of the two fragment types were not statistically different [ANCOVA, equal slopes,  $F_{(1,117)}=2.42$ ,  $P=0.12$ ; intercepts equal,  $F_{(1,117)}=0.22$ ,  $P=0.4$ ], and consequently, transport rates did not differ either [Fig. 4; slopes equal,  $F_{(1,117)}=2.82$ ,  $P=0.10$ ; intercepts equal,  $F_{(1,117)}=2.42$ ,  $P=0.12$ ].

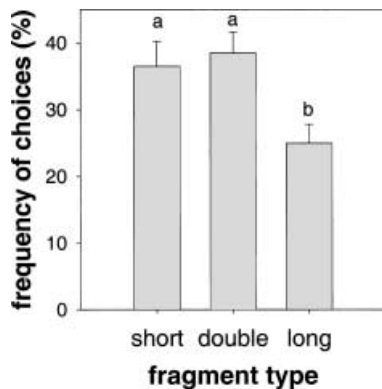
Fragment-size preference

Double fragments were chosen significantly more often than long fragments, despite their same mass (Fig. 5). In





**Fig. 4** Gross transport rate of foragers carrying fragments of different width (field measurements). Narrow fragments,  $y=113.87+9.63x$ ,  $r^2=0.30$ ,  $n=60$ ,  $P<0.0001$ ; wide fragments,  $y=159.99+4.71x$ ,  $r^2=0.08$ ,  $n=60$ ,  $P<0.05$ . The shaded boxes symbolise the two different fragment types used during the experiments



**Fig. 5** Load size preference of foragers in the field. The y-axis shows the mean percentage of choices  $\pm$  SE ( $n=20$  experimental series). Bars sharing the same letter are not significantly different (after one-way ANOVA)

addition, workers selected more often short rather than long fragments [one-way ANOVA,  $F=5.12$ ,  $P<0.01$ ; Newman-Keuls comparison,  $P<0.05$  for both cases]. No differences were found between the short and the double type of fragment (Newman-Keuls comparison  $P=0.7$ , not significant).

## Discussion

We investigated the economics of load transport in the grass-cutting ant *Atta vollenweideri* by focusing on the effects of load size (mass, length and width) on gross material transport rate to the nest. It was shown that for the same length, an increase in load mass led to higher transport rates even though workers ran at a slower pace. More marked were the effects of load length on transport rates when load mass was controlled for: an increase in load length led to significantly lower transport rates due to a major decline in transport speed. This indicates that length reduced manoeuvrability of the fragments during

transport, presumably by displacing the centre of gravity of the laden workers. In fact, we frequently observed that foragers carrying long grass fragments had difficulties in balancing the fragment and continuing walking, thus falling with their loads. This was less likely to occur with short fragments. The effects of load size on gross transport rate were observed over a wide range of forager sizes, as shows the comparison between laboratory and field experiments. Although forager size differed notably between laboratory and field colonies, load length significantly reduced both running speed and transport rate.

The negative effects of fragment size on transport rate, as described for grass-cutting ants, may not necessarily be marked in leaf-cutting ants harvesting leaf fragments that usually have a roughly semicircular shape. Since workers carry their fragments held more or less vertically overhead in a balanced position, an increase in fragment area is unlikely to cause a marked displacement of the centre of gravity during transport. Rudolph and Loudon (1986) showed that an experimental increase in the fragment masses carried by *A. cephalotes* foragers (without altering fragment area) also led to an increase in transport rate although running speed of the ants declined. Even though load mass did not affect manoeuvrability, the authors hypothesized that foragers would not select larger fragments because of the potential negative effects of wind during transport, at least for ants foraging in the canopy. But since transport occurs mainly along extended foraging trails on the floor, wind is unlikely to be significant for forest-inhabiting species.

The preference experiments statistically showed that when collecting dropped fragments, a situation that often occurs at harvesting sites where cutters drop fragments to the ground, workers discriminate among fragments of different length. Ants preferred short fragments, thus rejecting loads that are associated with long travel times and lower material transport rates. When collecting short fragments, they did not discriminate between different masses (single vs. double fragments). Therefore, workers did not select for maximal gross material transport rate, but for manoeuvrability and transport speed. This supports the idea outlined above that short travel times are highly relevant during foraging. Short travel times, besides the advantage of being associated with high material transport rates as shown in our experiments, might also favour recruiting activity (Roces and Hölldobler 1994; Roces and Núñez 1993), or contribute to the avoidance of parasitic attacks (Feener 1990). In the field, we frequently observed attacks by parasitic phorid flies, even during night. Under conditions in which a short travel time is important, it might be crucial for *A. vollenweideri* foragers to choose preferentially short fragments.

So, why do they carry long fragments at all? The crucial fact seems to be that cutting is an extremely energy-consuming process (Roces and Lighton 1995), particularly in grass-cutting ants harvesting monocots. For instance, *A. vollenweideri* foragers mostly need 10–30 min

to cut a single fragment of *Cyperus*, and many ants have been observed to give up before completing the cut (unpublished data). If only cutting energetics are considered, the longer a grass fragment, the larger the amount of material harvested per unit cutting effort. The consequence of this is that cutting length, i.e. grass width, remains more or less invariable irrespective of the fragment size cut (grass width usually changes abruptly only at the blade end). Based on these considerations, workers should be expected to cut very long fragments. But long fragments, as shown in the present study, have a detrimental effect on gross material transport rates when carried to the nest. The size of the fragments cut by grass-cutting ants under natural conditions may represent the outcome of an evolutionary trade-off between maximizing individual harvesting rate per unit effort during cutting, and minimizing the effects of fragment size on material transport rates.

The mechanisms involved in load-size determination by grass-cutting ants are completely unknown. The fragment lengths harvested in the field are larger than the maximal reach of workers, so they do not anchor their hind legs at the grass end while cutting. This implies that the mechanism of fragment-size determination is not a simple function of body geometry. Van Breda and Stradling (1994) found that *Atta cephalotes* workers, while cutting semicircular fragments, do not adjust the radius of cut to compensate for experimental changes in fragment weight during the process of cutting, i.e. workers do not assess directly fragment mass while cutting. They may use leaf toughness as an indirect measure, so as to decide about the size of their semicircular fragments. It is tempting to speculate that an analogous mechanism may underlie load-size determination in grass-cutting ants. If so, workers may decide, based on grass toughness, how large (long) the fragment to be cut should be, in order to select a fragment mass that does not negatively influence material transport rates. Experiments focusing on the mechanisms underlying fragment-size determination by grass-cutting ants are already under way.

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