Cutter, carriers and bucket brigades...

Foraging decisions in the grass-cutting ant

Atta vollenweideri

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Contents

Introduction

Social insects are particularly interesting for studies on decision-making, because they make choices not only as individuals in accordance to their own benefit, but each option contains a collective dimension and may concern the well-being of the colony. Even more, their fitness relies on the vitality of this “superorganism” (Seeley 1989a) since reproduction is largely restricted to the queen and their mates which in turn depend on the colony for their survival (Hölldobler and Wilson 1990; Oster and Wilson 1978; Wilson 1971). As a consequence, behaviour in social insects is expected to be adaptive on the colony’s perspective rather than on individual level. Under certain circumstances, individual behaviour may even be “suboptimal” or “inefficient” if considered as a single event, and its benefit may only be unveiled considering the overall state of the colony (Núñez 1982; Roces and Hölldobler 1994; Roces and Núñez 1993). Yet at least in large colonies, the individual must make its choices without having knowledge of the overall state and without the existence of a central control giving advises (Deneubourg *et al*. 1989; Robinson 1992; Seeley 1989a; Wilson and Hölldobler 1988). Instead work is self-organised (Bonabeau *et al*. 2000; Bonabeau *et al*. 1997; Deneubourg *et al*. 1987) and workers often follow rather simple behavioural rules based on cues of their direct environment (e.g. Deneubourg and Goss 1989; Gordon 1996; Gordon and Mehdiabadi 1999; O´Donnell 2001; Robinson 1992; Seeley 1995). One of the most fascinating features of the behaviour of eusocial insects is that despite these simple rules, highly complex patterns may emerge, e.g. in the construction of nests (Franks and Deneubourg 1997; Franks *et al*. 1992), or that the colony is capable to take collectively sophisticated decisions balancing several parameters against each other, for instance when new nest sites have to be chosen (Camazine *et al*. 1999; Mallon *et al*. 2001; Seeley and Buhrman 1999).

Foraging similarly demands a wide range of behavioural decisions taken by the individuals, such as where to forage, which sources or which item size, and each choice adds a piece to the huge mosaic called foraging strategy or – if the point of view is a more evolutionary one – colony fitness. However, foraging behaviour does not only include the collection of food but also the transmission of information about its location and quality (von Frisch 1965; Hölldobler and Wilson 1990; Wilson 1971). Because colony food intake is increased through recruitment communication, even at the expense of reduced foraging performance of the individuals, there may be a trade-off at the individual level between time spent either in acquiring food or in recruiting nestmates (Núñez 1970; Roces and Hölldobler 1994; Roces and Núñez 1993). This may be especially evident during the initial phase of exploiting a food source, when workers need to establish a foraging column in order to quickly monopolise the discovered food source.

This thesis seeks to enlighten foraging decisions and their adaptive value in eusocial systems on the example of grass-cutting ants, *Atta vollenweideri* (Attini). This species occurs in the

Chaco region of north Argentina and Paraguay and harvests monocots that serve for the cultivation of a symbiotic fungus within the nest, the main alimentation source of larvae and queen (Jonkman 1976). In contrast to the leaf-cutting species *A. sexdens*, *A. cephalotes* or *A. colombica* little is known about their foraging mechanisms, yet cutting monocots implies several features which strongly distinguishes them from leaf cutters. The first chapter therefore provides a detailed description of the cutting behaviour and the effect of the toughness of the tissue that has to be cut on fragment size determination. The second chapter analyses the effect of distance from the nest on load size, and deals with the question whether fragment size determination of individual foragers changes during transport. Why such changes regarding load size may be relevant for the individual as well as for the colony, I investigate in the third chapter, turning the focus on transport economics and the effect of load length, width and mass on running speed – the individual trait – and gross material intake rate – the collective trait.

Large colony size and worker size polymorphism may allow a high degree of specialisation and division of labour within a colony (Jeanne 1986a; Robinson 1992). Indeed, worker size polymorphism generally is correlated with worker specialisation (Hölldobler and Wilson 1990). Chapter four and five therefore investigate how foraging is divided into several tasks, which specialisation occurs and how it is related to worker size. In chapter four I present the pattern of foraging and the effect of trail length, and I introduce the phenomenon of transport bucket brigades, i.e. a fragment is carried consecutively by several workers. In chapter five I analyse the adaptive value of these bucket brigades by testing the predictions of two hypotheses. Finally in chapter six, I compare division of labour and the occurrence of bucket brigades of *A. vollenweideri* and the less polymorph leaf-cutting species *Acromyrmex lundi* and follow the question what triggers the formation of bucket brigades.

Cutting behaviour and fragment-size determination in the grass-cutting ant *Atta vollenweideri*

Summary. This field study focuses on cutting behaviour and decision-making by foraging grass-cutting ants, *Atta vollenweideri*. It first presents a detailed description of cutting behaviour and the effects of ant body size, and further addresses the question of fragment size determination when foragers cut fragments from grasses of different toughness. Foragers were observed to cut grass fragments across the blade, thus resulting in longish, rectangular-shaped fragments. Cutting was very time-consuming, with cutting times lasting up to more than 20 minutes per fragment. Roughly half of all initiated cutting attempts were prematurely broken off by the ants, which usually searched for another cutting site afterwards. Most ants only managed to cut one complete fragment during the observation time, and the probability of terminating the cutting site, if the ant initiated a second cut, was significantly higher in the second attempt than in the first one. No relationship was found between the number of cutting attempts, the number of successful cuts or the probability of giving up a cutting site and the body size of the forager. Cutting time was greater and cutting speed was slower when foragers cut a denser (i.e., harder) grass, in spite of the fact that the ants were larger than those foraging on soft grasses. For both the hard sedge *Cyperus entrerrianus* and the soft grass *Leersia hexandra*, cutting speed correlated with ant body mass. The length of the fragments cut out of the two grass species differed statistically, but showed a large overlap in their distribution. Fragment length correlated with ant body mass for both grass species, yet with a very small correlation coefficient, indicating little biological significance of this relationship. Fragment width correlated with ant body mass for the hard grass but not for the soft one, suggesting that when cutting is difficult, larger ants tend to select wider grasses to initiate cutting.

Introduction

Leaf-cutting ants of the genus *Atta* harvest large amounts of plant material that they process in the nest into a humus-like substrate serving for the cultivation of a symbiotic fungus (Weber 1972). The ellipsoidal swellings of the fungus hyphae, the “gongylidia”, represent the main food source of queen and larvae, whereas workers mainly feed on plant sap (Bass and Cherrett 1995; Littledyke and Cherrett 1976). The marked body size polymorphism and the elaborate division of labour system enabled them to become the most important herbivores of the New World Tropics and Subtropics, conquering a diversity of habitats with their enormously sized colonies (Hölldobler and Wilson 1990; Wilson 1983a; Wilson 1983b). Colonies establish extended trail systems that direct columns of thousands of workers to the food patches, allowing foragers to travel faster than on areas covered with vegetation (Howard 2001). Their foraging can have a devastating effect on agricultural plantations, hence they are considered to be severe pests in Central and South America (Cherrett 1986; Fowler *et al*. 1986; Hölldobler and Wilson 1990; Robinson and Fowler 1982), but they also have a high ecological relevance for instance with regard to both plant growth and succession (Haines 1978; Jonkman 1978).

Based on the mode of cutting, one can roughly distinguish two different groups within the genus *Atta*: Workers belonging to the well-studied species *A. cephalotes*, *A. sexdens* or *A. colombica* cut approximately semicircular leaf fragments. These species mainly occur in forests and harvest on trees or other dicots, neglecting monocotyledonous food sources, and are therefore referred to as “leaf-cutters” (Fowler and Stiles 1980; Wetterer 1991b; Wetterer 1995). In contrast, *A. vollenweideri*, *A. capiguara* and *A. bispherica* belong to a group of species which mainly cuts monocots and only rarely harvests dicots, therefore referred to as “grass-cutters” (Fowler *et al*. 1986; Jonkman 1976; Jonkman 1980).

Leaf-cutting ant foragers exhibit an elegant cutting technique that allows them to determine and adjust the size of the fragment they cut: Workers anchor themselves with their hindlegs at the leaf edge and rotate during cutting, thus giving fragments their semicircular shape. Maximal fragment size is limited by the reach of the ant while cutting, and it therefore correlates with ant body size (Lutz 1929; Weber 1972). Yet, absolute fragment sizes are also influenced by leaf density (Breda and Stradling, 1994; Cherrett, 1972; Roces and Hölldobler, 1994; Rudolph and Loudon, 1986), by the information about resource quality workers received before cutting (Roces 1993; Roces and Núñez 1993), as well as by the state of the colony as a whole (Roces and Hölldobler 1994). Grass-cutting ants, in contrast, cut straight across the grass blade, which results in the harvesting of roughly rectangular fragments. 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. Daguerre (1945) described the usual fragment lengths cut by workers of *A. vollenweideri* as having a mean of 43 mm. The mechanisms involved in load-size determination by grass-cutting ants are completely unknown. One would expect fragment length to be determined by the foragers, as load length has a marked detrimental effect on travel speed and, as a consequence, on material intake rate: by keeping load mass constant, longer loads were observed to be carried slower, thus yielding lower transport rates, than shorter loads (Röschard and Roces 2002c; Chapter 3).

In this study I present the first detailed description of cutting behaviour of the grass-cutting ant *Atta vollenweideri*. In the field, I marked individual foragers during cutting and observed their subsequent behaviour, focusing on their cutting technique, time investment, and cutting success. I finally focused on the question of fragment size determination and the correlation between fragment size and ant body size for two different grass species differing in their area density, thus investigating possible effects of tissue toughness on decision-making.

Material and Methods

Cutting behaviour

Experiments were conducted at the ranger station Estero Poí in the National Park Río Pilcomayo in Formosa province, Chaco region of north Argentina, between October 1998 and May 1999, on a two to three year old colony of *Atta vollenweideri*. Most observations were performed during the night by using red light.

In order to have a restricted foraging area that makes observations of single foraging workers possible, a circular area of ca. 1.5 m in diameter was defined at a distance of 5 m from the nest, next to an existing trail of 35 m total length. A plastic fence of approx. 40 cm height treated with plant oil, in order to avoid escape of the ants, surrounded the 5 m trail sector and the foraging area. The original trail was connected with the enclosed trail sector by wooden bridges, so as to regulate the number of foragers collecting outside or inside the food arena during the observations. The area was completely cleared and only few grass plants of *Paspallum intermedium*, a species frequently harvested by the ants, were transplanted about half a day before an experimental series, in order to standardise the plants provided each experimental day. Before foraging activity started, the grass blades were treated with an orange juice solution (50% orange juice in water), so as to increase their attractiveness. In order to have a quantitative measure of grass toughness, the tissue area density (mass/surface area) was calculated. Four samples of a newly transplanted plant provided a mean area density of 0.16 ± 0.02 mg/mm^2, thus *Paspallum intermedium* had a toughness between the “soft” and “hard” grasses that will be described below.

A total of 22 randomly chosen foragers were marked with a small colour dot (Edding® paint marker 780 or liquid TippEx®), shortly after they had started cutting. Only ants that did not show any signs of alarm were followed. Ants were observed for at least 45 minutes since the beginning of cutting except those ants that returned to the nest earlier. For two ants the observation period lasted only 25 and 30 minutes because I lost sight of them. In order to determine the body size of the foragers, their maximal head width was measured during cutting to the nearest 0.25 mm by comparing them with a template of fixed ants of known sizes.

Fragment size determination

Investigations of fragment size determination by *A. vollenweideri* foragers were conducted in the biological field station of the “Reserva Ecológica El Bagual” in Formosa province, Chaco region of north Argentina, in October 2000 on a three to four year old mature colony. All observations were performed during the night by using red light. In order to assess the effects of grass area density, measurements were taken from two different plant species frequently harvested by the ants, the sedge *Cyperus entrerrianus* (henceforth: “hard grass”), with a mean area density of 0.24 ± 0.12

mg/mm^2 (n=108), and the grass *Leersia hexandra* (henceforth: “soft grass”), with a mean area density of 0.10 ± 0.03 mg/mm^2. Foragers harvested on *Cyperus entrerrianus* at 8 metres and on *Leersia hexandra* at 15 metres from the nest. Ants that climbed on a grass blade and searched for a site to initiate cutting were observed and their cutting time recorded. After cutting, ants were collected together with their fragments. Ant and load mass was then determined to the nearest 0.1 mg, and load length and width to the nearest 0.5 mm. Ambient temperature and humidity ranged from 12.5 to 28.2 °C for the hard grass and from 19.5 to 23.8 °C for the soft grass. Humidity ranged from 75 to 99%.

Statistical analyses were done using the Statistica® software. Correlation was tested with the Spearman Rank Correlation Test, and differences between samples with the Mann-Whitney-U-Test, as samples with significant and non-significant relationships had to be compared and regression analysis was therefore not possible.

Results

Cutting behaviour

Body size of the observed ants ranged from 1.5 to 3.0 mm head width, with most ants having head widths from 1.5 to 2.25 mm. In order to convert this measure into body mass, both head width and body mass of 85 ants spanning over the whole size range were measured. Using these measures, body mass was observed to vary from 5.5 to 27 mg, with 86 % of the workers ranging from 5.5 to 15.5 mg.

The process of leaf harvesting could be conveniently divided into an initial searching phase, in which ants walked rather quickly along a grass blade and then moved to neighbour blades of the same plant, and a “testing” phase in which ants walked slowly on a given grass blade, steadily probing it with the mandibles. Typically, ants repeatedly moved to the tip of the blade and after biting into it walked downward again. They walked up and down the upper part of the grass blade several times before they started cutting. Cutting behaviour was considered to begin when a noticeable cutting movement lasted at least 20 seconds. Otherwise it was considered as “testing” and not included in the following analyses.

I first analysed the number of fragments an ant harvested during observation time. Thirteen out of 22 ants (59 %) succeeded in cutting only one complete fragment during the observation time, 4 ants (13 %) even returned to the nest without having succeeded at all, and only 3 (14 %) ants managed to cut more than three fragments. Thus, most ants cut only one or two fragments during observation time. However, most ants made one or two further cutting attempts which they abandoned again. No relationship was found between ant body mass and the number of fragments cut or with the number of abandoned cuts (Fig. 1).

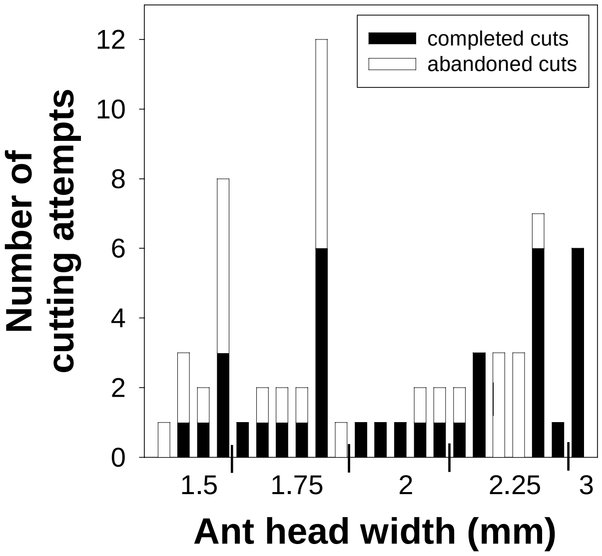


Fig. 1:
Number of cutting attempts on *Paspallum intermedium* for each observed forager. Black bar sections indicate cutting trials in which ants succeeded. White bar sections indicate the number of cutting attempts abandoned by the ants. The numbers on the x-axis indicate the upper limit of the head width intervals considered, i.e. the bar labelled with “1.75” includes all head widths larger than 1.5 mm up to 1.75 mm.

Why is the number of fragments cut by the ants so low? Possibly the probability that an ant initiates a cut declines, the longer it forages or the more fragments it already has cut, e.g., because of physical exhaustion. Ants that foraged for longer times would be expected to return to the nest, whereas ants that harvested for shorter times may continue cutting. Thus, if the number of harvested fragments was low because ants were already cutting for a long time or got exhausted, I would expect that this mainly refers to those foragers returning to the nest. I do not know how long workers had been foraging when our observation started, but some ants returned to the nest during our observation whereas others continued foraging. If I focus only on those workers that returned to the nest, the number of harvested fragments remains similar: Six of the ten foragers succeeded in cutting one fragment (60%), whereas two returned to the nest without finishing a cut, and two others cut more than three fragments (20% each). Hence, irrespective whether ants ceased or continued foraging, they mostly cut only one fragment.

Foragers generally needed 5 to 15 minutes to perform a complete cut of a fragment from *Paspallum intermedium*, but in some cases cutting times of 20 minutes or more occurred (Fig. 2). I regularly observed ants sitting entirely still without any visible cutting movement after having cut a short length, thus possibly recovering before resuming cutting. This “resting behaviour” lasted approximately 10 to 60 seconds. In addition, ants frequently showed brief “interruptions” during their cuts, which differed from the resting behaviour in that foragers released the grass blade they were cutting. I observed two types of interruptions: In some cases ants briefly released the blade for a few seconds, while they kept sitting without any visible movement. In other cases they walked once or several times to the tip of the grass blade and returned subsequently to the cutting site, thus repeating the behaviour displayed during the testing phase. In most cases only one interruption occurred, but up to five were observed. Both resting time and interruptions were included in the cutting time.

A considerable number of cutting attempts was unsuccessful: I observed a total of 66 initiated cuts of which ants abandoned 29, i.e. 44%. Most cutting attempts were abandoned during the first five minutes of cutting but sometimes foragers cut 15 minutes or more before giving up (Fig. 2). Interestingly, the probability that a cut was abandoned was related to the occurrence of interruptions. I observed 29 abandoned cuts of which 13 were interrupted during cutting, thus 45% of all abandoned cuts were interrupted during cutting. Conversely, 10 of 37 complete cuts were interrupted, thus only 27% of all complete cuts were interrupted. Hence, abandoned cuts were slightly though not significantly more often interrupted than complete cuts despite their lower cutting time (see Fig. 2) (Fisher’s exact test, p=0.06).

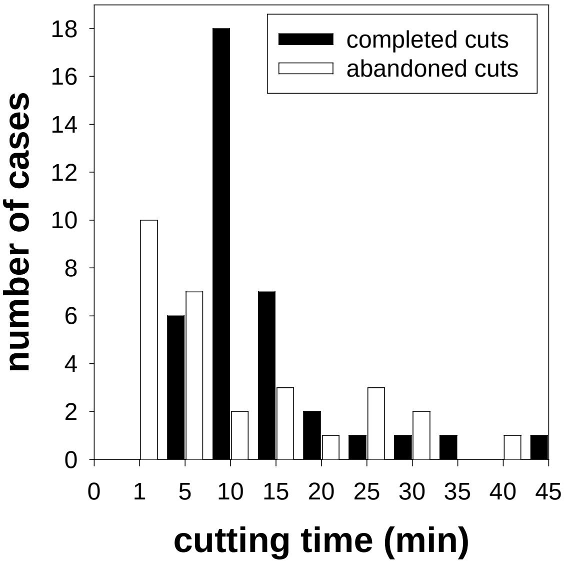


Fig. 2:
Cutting time of *Atta vollenweideri* foragers cutting on *Paspallum intermedium*. The dark bars indicate the number of observations in which a cutting attempt was successful, i.e. the ant completed the cut. White bars show the cases in which ants gave up after the specified time. The numbers on the x-axis indicate the upper limit of the time range considered, i.e. the bars centred on “5 min” represent the number of ants that cut (or gave after) one to five minutes.

I mentioned above that cutting success, i.e. the probability to complete a cut, might decline, the longer an ant was involved in harvesting. I therefore compared cutting success during the first cut (observed by us) and the following cuts. 15 of the 22 observed ants initiated a second cut and 8 a third one. Seventeen (77 %) foragers were successful during their first cutting attempt. Only four ants (28 %) were successful during their second cut and three (38%) during their third cut. Therefore cutting success indeed declined after the first harvested fragment. (Chi-Square-Test: first vs. second: χ^2=9.31, p<0.005); first vs. third: χ^2=4.18, p<0.05; second vs. third: χ^2=0.29, p=0.6, NS) (Fig. 3).

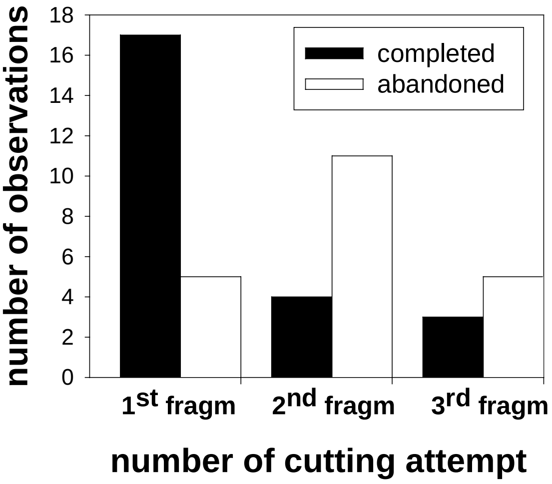


Fig. 3:
Probability of successful or unsuccessful cuts in consecutive cutting attempts on *Paspallum intermedium*. Whereas most ants complete their first cut, most second or third cutting attempts were given up.

The probability that a cut is successful might depend on the time an ant had for recovering before initiating a new cut. I therefore compared recovering times before successful and before unsuccessful cuts. There was no significant difference (Mann-Whitney-U-Test: U=145, p=0.09, NS). Furthermore, the time an ant is able to cut might rely on the recovering time, i.e. the time spent without cutting, before a cut. Conversely, after a long cutting time, ants might need a long recovering time before being able to initiate another cut. I therefore analysed the possible relationship between cutting time and the recovering time before and after the cut. There was no significant relationship (Spearman rank correlation test; time before vs. cutting time: t=1.5, n=41, p=0.1, NS; cutting time vs. time after: t=1.0, n=28, p=0.3, NS; data for complete and abandoned cuts were pooled, separate analyses also showed no significant differences).

Fragment size determination

Foragers cutting the hard *C. entrerrianus* ranged from 5.9 to 58.5 mg (median: 12.9 mg, n=79), and were significantly larger than foragers cutting the soft *L. hexandra*, which ranged from 2.1 to 17.6 mg (median: 6.3 mg, n=102; Mann-Whitney-U-Test: U=938, p<0.0001). In addition, variance was much higher for foragers cutting the hard grass (Quartile ranges; hard grass: 7.9, soft grass: 3.4).

Most of the ants needed 10 to 30 minutes for cutting a single fragment of *C. entrerrianus*, with a considerable number of ants cutting much longer. When cutting *L. hexandra*, however, ants generally spent less than 5 minutes, with a large number of ants cutting 2 min or less (Fig. 4). Cutting speed significantly correlated with worker size for both plant species, yet significance was much stronger for the hard grass (U-Test: U=337, $n_{(hard)}=52$, $n_{(soft)}=62$, $p<0.0001$; Spearman rank correlation: hard grass: $r^2=0.49$, $t=7.82$, $p<0.001$; soft grass: $r^2=0.13$, $t=2.32$, $p<0.05$). As expected, cutting speed was much higher for the soft *L. hexandra* (Fig. 5).

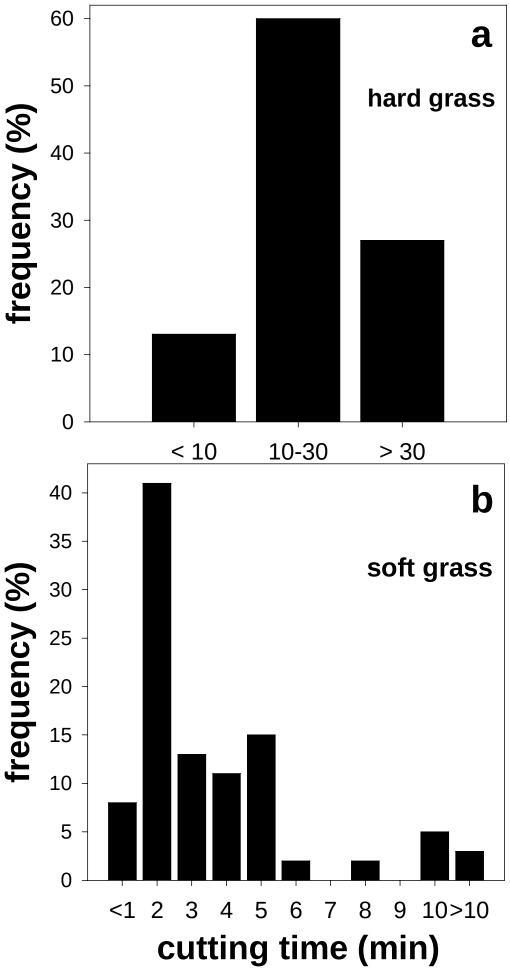


Fig. 4:
Cutting times spent by workers when cutting fragments out of the hard *Cyperus entrerrianus* (a) or the soft *Leersia hexandra* (b). Note the different scaling on the X-axes. The Y-axes show the percentage of observed ants cutting for the specified time.

Cutting speed might be expected to decline with increasing cutting length, as the ant's energy reserves might be used up. In this case, the measured speed should be expected to decline with increasing fragment width, at least for the hard grass with its high variance of blade widths. Yet, this was not the case (t=1.78, n=52, p=0.08, NS). Similarly, if analyses were restricted to ants of similar size (between 10 and 15 mg body mass), there was no significant relationship between cutting length and cutting speed (t=1.43, n=22, p=0.17, NS).

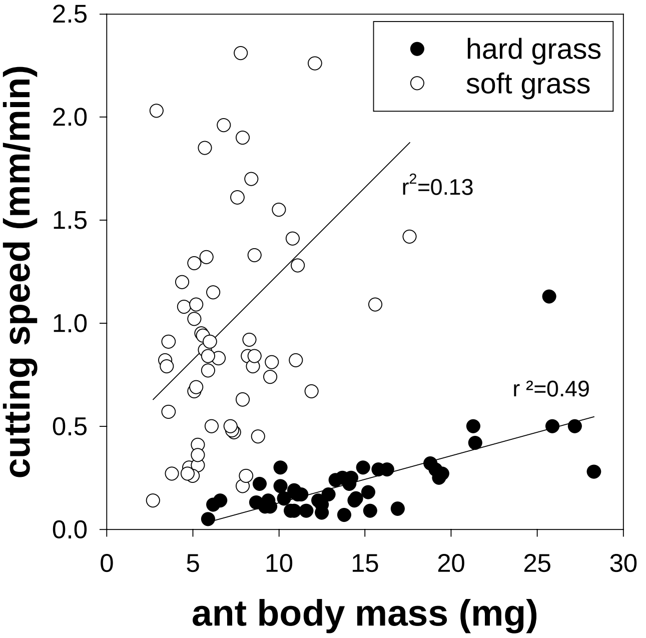


Fig. 5:
Cutting speed of foragers harvesting on the hard *C. entrerrianus* or the soft *L. hexandra*.

The length of the fragments cut from *C. entrerrianus* was significantly larger than those of *L. hexandra* (U-Test: U=2196.5, $n_{(hard)}$=80, $n_{(soft)}$=102, p<0.001). It is important to note, however, that whole leaf blades of the latter did not exceed 100 mm and most of them maximally measured 60 to 80 mm. Fragment length correlated significantly with ant body mass in the soft grass, but with a very small correlation coefficient (Fig. 6a; r^2=0.05, t=2.63, n=101, p<0.01). No correlation was found for the hard grass (Fig. 6a; t=1.33, n=79, p=0.2, NS).

Fragment of *C. entrerrianus* were significantly wider than those of *L. hexandra* (U=1024.5, $n_{(hard)}$=80, $n_{(soft)}$=101, p<0.0001). Fragment width correlated significantly with ant body mass for the hard grass but not for the soft one (Fig. 6b; hard grass: r^2=0.10, t=4.33, n=79, p<0.0001, soft grass: t=1.54, n=100, p=0.1, NS). This might be due to the small range of widths occurring in *L. hexandra*.

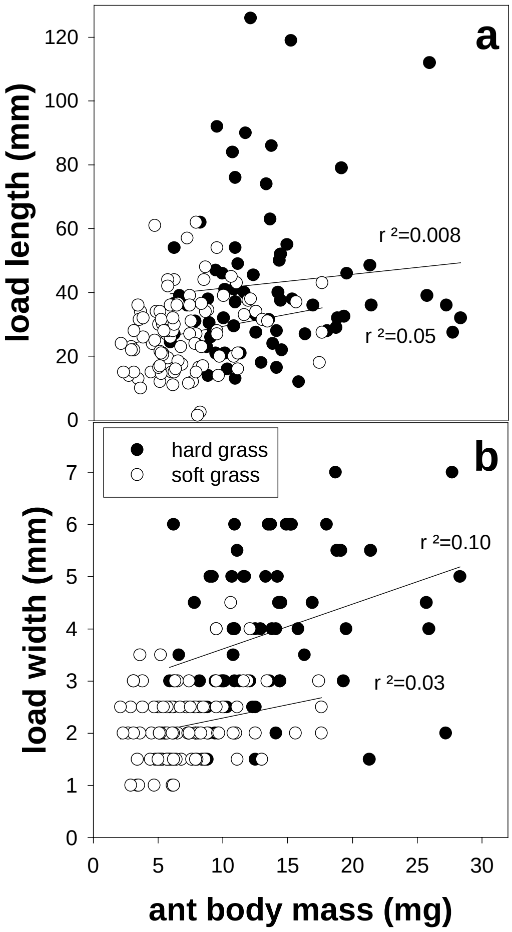


Fig. 6:
Correlation between ant body mass and fragment length (a), and fragment width (b). Foragers were harvesting on *C. entrerrianus* ("hard grass") and *L. hexandra* ("soft grass").

As fragment length and width differed in the two grass species, load mass differed as well: Fragments from *C. entrerrianus* were heavier than those from *L. hexandra* (Fig. 7a; U-Test: U=154, $n_{(hard)}$=80, $n_{(soft)}$=103, p<0.0001). Fragment mass correlated significantly with ant body mass, but the correlation coefficients were low in both cases (hard grass: r^2=0.05, t=4.01, n=79, p<0.0005; soft grass: r^2=0.05, t=2.53, p<0.05). The same is true for fragment surface area: Fragments of the hard grass were larger than those of the soft grass (Fig. 7b; U=815.5, $n_{(hard)}$=80, $n_{(soft)}$=98, p<0.0001). Both correlated significantly with ant body mass (hard grass: r^2=0.05, t=3.58, p<0.001, soft grass: r^2=0.08, t=3.15, p<0.005), yet with a very low correlation coefficient that indicates only little biological relevance of this relationship.

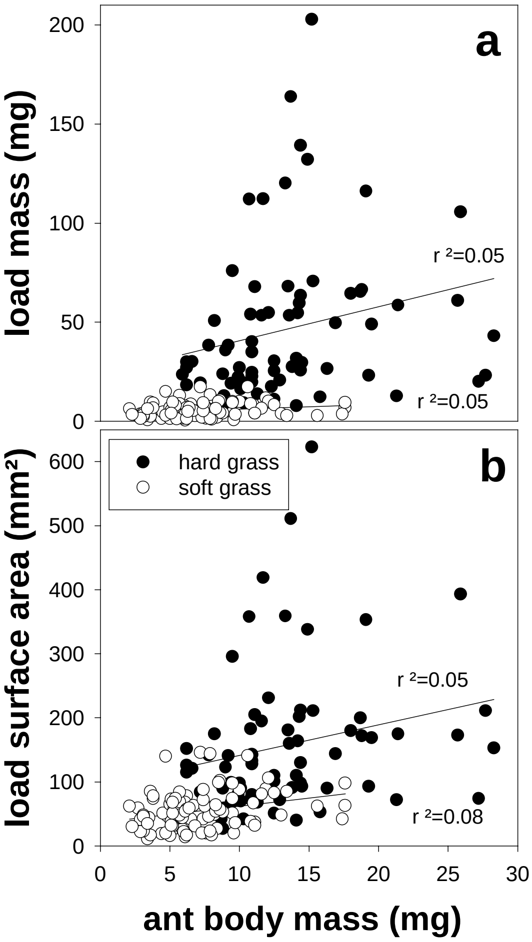


Fig. 7:
Correlation between ant body mass and fragment mass (a), and surface area (b). Foragers were harvesting on *C. entrerrianus* ("hard grass") and *L. hexandra* ("soft grass").

Discussion

Foragers of grass-cutting *Atta vollenweideri* cut rectangular-shaped fragments by cutting straight across the grass blade. Thus, in contrast to leaf-cutting *Attine* species like *Atta sexdens*, ants cannot determine fragment size using their body as a pivot when anchoring themselves with their hindlegs at the leaf edge (Lutz 1929; Weber 1972). They must apply a different technique that may be connected with the pronounced pattern of searching along a grass blade before they begin. By walking along a grass blade and especially by walking down from the tip, ants might be able to assess the distance covered, so as to obtain information about the length of the fragment they are going to cut. Interestingly, ants showed the same behaviour before cutting, i.e., walking along a grass blade from one end, even if the grass blade was lying on the ground but was too large for carrying.

If ants assess length by walking along the blade, one might *a priori* expect a correlation between ant size and fragment length. This was only the case in the soft grass *L. hexandra*, but neither in the hard grass *C. entrerrianus* nor in the medium *P. intermedium*. However, even in *L. hexandra* the correlation of ant size and fragment length only explains five percent of the variation, thus indicating little biological relevance of body size on the decision about the fragment length to be cut.

In general, fragment lengths varied between 10 and 65 mm for the three plant species investigated, which have very different tissue area densities, and thus corresponded roughly to the mean values of 43 mm reported by Daguerre (1945). In both *C. entrerrianus* and *L. hexandra*, a large number of fragments was longer than 40 mm, yet foragers had obviously difficulties to handle and manoeuvre them, so that they are usually cut again (unpublished observations). Fragment length represents a severe constraint for the economics of load transport in *Atta vollenweideri*. It was recently shown that running speed and therefore material intake rate strongly declined with increasing load length, independent of load mass (Röschard and Roces 2002c; Chapter 3).

This limitation becomes important when the energetic of leaf cutting is considered. Cutting was shown to be an energetically intense process with metabolic rates being about 30 times higher during cutting than during resting (Roces and Lighton 1995). Based on the energetic of cutting, workers might maximise 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. Therefore it would be advantageous for the ants to cut long fragments and save the effort of another cut. Our study reveals that time also represents a further important constraint. In the typical grassland species *Paspallum intermedium* and *Cyperus entrerrianus*, ants needed often longer than 20 minutes to cut a single fragment. I frequently observed that ants stood still during cutting without any visible movement, possibly resting. It might be interesting to investigate whether metabolic rates indeed drop during these “resting times”, indicating that ants in fact need to recover.

Thus cutting requires a high investment of energy and time but in addition, nearly half of the cutting attempts on *Paspallum intermedium* and an approximately equal proportion at *Cyperus entrerrianus* (unpublished) were given up, and most foragers did not succeed to cut more than one or two complete fragments within observation time. I do not know how long the observed foragers had already been active, nor do I have data of workers that had just started foraging. But our data on ants that returned to the nest, and on those which continued foraging, showed an amazingly low number of successful cuts, thus suggesting that foragers in general cut only very few fragments during a foraging cycle.

Ants were significantly more often successful during their first (observed) cut than during the following one, indicating that most ants did not manage to cut another fragment. Why do ants give up cutting sites so often? As argued above, the most conceivable reason might be the fatigue of the forager. Monocot species like *Paspallum intermedium* and *Cyperus entrerrianus* are hard and have very tough veins, and ants were often observed to spend a considerable proportion of their cutting time at the mid vein. Possibly ants left after their energetic reserves were used up. This is in congruence with the observation that in the soft grass ants only gave up in 5 to 10 % of the cases (unpublished observations). Considering the effect of fatigue, one might suspect that the time spent recovering before starting a second cut should have some influence on both the probability of being successful and the time spent cutting, yet this was not the case. Nor was there a correlation between the cutting effort and the time spent "recovering" after the cut.

Another more speculative explanation for the high frequency of terminating cutting sites might be a fast defensive reaction of the plants. Plant selection by leaf-cutting ants is markedly influenced by the secondary chemistry of the plants (Cherrett 1972; Howard 1988; Littledyke and Cherrett 1976; Vasconcelos and Cherrett 1996), and by the digestibility of the material by the fungus (Lapointe *et al*. 1996). Grasses are also known to contain antiherbivore substances (Vicari and Bazely 1993), and at least in some cases they seem to be able to rapidly respond to stress by modifying tissue chemistry (reviewed in Karban and Myers (1989). Whether savannah grasses like *Paspallum intermedium* are similarly able to chemically respond within several minutes or hours remains unknown. However, as ants were frequently observed to switch to neighbour plants before having depleted the plant actually harvested, the presence of chemical antiherbivore defences cannot be ruled out.

Based on time and energy investment, it appears intuitive that most of the foragers cutting the hard *C. entrerrianus* were large, and that small foragers were absent. Possibly the latter ones left the plant after being unable to cut. More striking is the fact that in the soft *L. hexandra*, large ants were absent, thus worker size distribution was narrower in the easy-to-cut vegetation than in the hard grass, which is exactly the opposite to what one intuitively would expect. Similar effects were found for *A. cephalotes* (Rudolph and Loudon 1986) and *A. sexdens* (Wilson 1983b) with larger ants cutting denser vegetation. Whether the ultimate advantage of "reserving" larger workers for cutting hard vegetation appears appealing, the proximate mechanism underlying such a shifting remains unknown. Wilson (1983c) suggested for *A. sexdens* that larger ants tend to abandon cutting sites if disturbed by smaller ants. Whether this mechanism applies for *A. vollenweideri* remains obscure.

Ants walking along a grass blade usually touch both edges of the blade with their tarsi. If they are prevented to clasp both edges simultaneously, they were observed to cut semicircular fragments (like *A. sexdens* cutting dicots) and not across the blade width as they usually do (unpublished). Hence, they appear to respond to grass width. Based on size, one might expect larger ants (with larger mandibular muscles) cutting preferentially wider fragments. For the hard *C. entrerrianus*, this relationship was found to be significant. The proximate mechanisms are unknown, but it may be argued that ants should prefer to initiate cutting at places where they can efficiently clasp the blade, so that they sort out themselves in relation to blade width. Such correlation was absent in ants cutting the soft grass, possibly due to the small range of widths available.

Both load mass and load surface area showed a clear correlation with ant size, with the larger ants cutting larger fragments. Yet, it does not seem conceivable that ants can assess or respond to load mass during cutting. 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 to assess the size of their semicircular fragments. Regarding grass-cutting ants, it appears that the relevant variable for the determination of grass fragment size is the length. The negative effects of load length on transport (Röschard and Roces 2002c; Chapter 3) might restrict ants to select fragments within a certain length range irrespective of width, area density or plant species.

Fragment-size determination and size-matching in the grass-cutting ant *Atta vollenweideri* depend on the distance from the nest

Summary. Fragment size-determination by workers of the grass-cutting ant *Atta vollenweideri* and the extent of size-matching between ant size and fragment size were investigated as a function of the distance from the nest. Foragers and their loads were sampled in 4 different sectors along a 30 m foraging trail in the field: directly on the harvested plant, at the patch, on the trail and close to the nest. Ants sampled on the plants immediately after cutting were significantly larger than carrying ants on any trail sector, whereas body mass did not differ among other groups. Thus, foraging was partitioned in at least two stages, with large ants cutting the plants and smaller ants carrying the fragments to the nest. Fragments collected directly after cutting were significantly larger than those carried on the trail, indicating that the fragments were cut once again on their way to the nest. Size-matching depended on the trail sector considered, and was stronger in ants sampled closer to the nest, suggesting that carriers either cut fragments in sizes corresponding to their body mass prior transport, or transferred them to nestmates of different size after a short carrying distance. The hypothesis that long grass fragments are cut in transportable length prior to carrying was tested in the laboratory. The probability of cutting a dropped fragment depended on its length. Fragments with lengths up to 40 mm were cut into halves, so that workers selected a *relative* length to initiate cutting. Conversely, workers cut pieces of an *absolute* length when finding longer fragments. These results indicate that workers make specific decisions when cutting fragments on the ground, but the measures used to determine the length of the piece to be cut depend on the assessment of total fragment length.

Introduction

Load-size selection in ants is a complex process influenced by different variables such as ambient temperature (Traniello *et al*. 1984), seasonality (Fowler and Robinson 1979), and food quality (Roces and Hölldobler 1994; Willott *et al*. 2000). When foraging, ants might not only decide about the absolute size of an item, i.e., whether to select a larger or smaller one, but might also select load sizes relative to their body mass. This size-matching, i.e., the correlation between ant body size and load size, has repeatedly been reported not only when monomorphic ants species of different size were compared (Davidson 1977; Kaspari 1996), but also for polymorph species such as seed-harvester ants (Kaspari 1996) and leaf-cutting ants (Cherrett 1972; Lutz 1929).

In seed-harvester ants, size-matching may result either from the selection of loads of appropriate size by workers that carry them, or indirectly when loads are transferred along the foraging trail to nestmates of different size (Reyes-López and Fernández Haeger 1999; Reyes-López and Fernández-Haeger 2001). However, a number of studies failed to find size-matching in harvester ants collecting seeds (Ferster and Traniello 1995; Rissing and Pollock 1984). It is important to point out that in these investigations, ants were collected near the food patch. Reyes-López & Fernández-Haeger (2001) recently showed that in the seed-harvesting ant *Messor barbarus*, size-matching was more significant along the trail because seeds were usually transferred to nestmates, indicating that both the criteria for load-size selectivity and the extent of size-matching depend on the distance from the nest.

In leaf-cutting ants, size-matching results from the geometric mode of leaf-cutting. Since workers anchor their hindlegs at the leaf edge and pivot around their body axis while cutting, their reach may be used as a reference during fragment-size determination, and in fact, larger ants were observed to harvest fragments of larger area (Lutz 1929; Weber 1972). Yet, fragment-size determination is flexible because ants can alter their reach while cutting, so as to cut smaller fragments, for instance as a function of leaf area density (Burd 1995; Cherrett 1972; Roces and Hölldobler 1994), or familiarity with the food source and state of the colony (Roces and Hölldobler 1994).

The mechanisms of fragment-size determination in grass-cutting ants, for instance in *Atta vollenweideri*, are rather different. 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. Since workers do not anchor their hindlegs at the grass tip, body size cannot be used as a reference during fragment-size determination as it is the case for leaf-cutting ants. Therefore, size-matching between ant and fragment size as a result of the geometry of cutting would not be expected. And in fact, there is no or only a weak correlation between ant size and load size for fragments collected directly at the cutting site in the field (Röschard and Roces 2002c; Chapter 3). However, if I consider that fragments are carried on foraging trails over considerable distances sometimes exceeding 100 m, size-matching may be important to enhance transport performance, which refers not only to energetic costs (Lighton *et al*. 1987), but also to time saving (Röschard and Roces 2002c; Chapter 3). Single foraging trips may require several hours on long trails, and since fragments are often observed to be transported sequentially by a number of workers, it is conceivable that size-matching improves as the fragments are passed on to other workers along the trail.

In order to investigate the rules used by workers when cutting grass fragments, and whether both the occurrence and strength of size-matching depend on the distance from the nest, fragment-size determination by the grass-cutting ant *Atta vollenweideri* was investigated in the field. Both ant and fragment sizes cut out of the sedge *Cyperus entrerrianus* were measured in different trail sectors. In addition, size-matching was investigated in workers cutting fragments of two grass species strongly differing in their tissue area density (mass/area), so that fragments of similar area will differ in their mass. As a consequence, potential effects of fragment mass and fragment area could be analysed separately. Finally, the hypothesis that long grass fragments are cut in transportable length prior carrying was tested in the laboratory by presenting workers fragments of different length and recording the probability of cutting and the lengths actually cut.

Methods

Field experiments were conducted on a mature colony of *Atta vollenweideri* at the biological field station El Bagual in Formosa province, Chaco region of North Argentina, in August 2000. Foragers harvested fragments of the hard sedge *Cyperus entrerrianus* (family Cyperaceae; tissue area density: 0.24 ± 0.12 mg/mm^2, mean ± SD, N=108) at a distance of 30 metres from the nest. The trail continued for about 15 metres more where ants foraged on a variety of monocots, predominantly on the soft *Leersia hexandra* (family Poaceae; tissue area density: 0.10 ± 0.03 mg/mm^2, mean ± SD, N=102). At the time of the experiments, *C. entrerrianus* plants had a height of 15 to 50 cm and had already been cut before.

In order to investigate whether fragment-size determination and size-matching depended on the distance from the nest, samples of foragers and their fragments cut out of *C. entrerrianus* were collected at four different trail sectors. The sedge *C. entrerrianus* was predominantly cut by the ants, and due to its green shiny colour and toughness, fragments were easily distinguished from other plant fragments transported along the same trail. The following places along the trail were selected for sampling: (1) the harvested plant, i.e., cutting ants were captured immediately after or shortly before finishing a cut (henceforth: "plant"); (2) the patch, i.e., samples were collected at a distance between 0.5 and to 1 m away from the harvested plant, while ants were walking on the ground before reaching the main trail (henceforth: "patch"); (3) the trail, 5 metres away from the harvested plant and 25 metres from the nest entrance (henceforth: "trail"). At this distance, all side trails with the exception of one with very low activity had met the main trail. (4) Two meters from the nest entrance (henceforth: "nest"). Sample size per sector ranged between 51 to 64 ants and their loads.

The effects of tissue area density on fragment-size determination and size-matching were investigated as follows. Fragments of the hard *C. entrerrianus* sampled at the nest were compared with an additional sample, also taken at the nest, of ants carrying the soft grass *L. hexandra*. For that, each third ant together with its load crossing a marked section of the trail was collected. Workers carrying *Cyperus* fragments, which were easily identified, were omitted. Since at the time of sampling workers also harvested fragments of a soft *Paspallum* grass on a secondary trail, it cannot be excluded that the sample of *L. hexandra* collected at the nest includes some *Paspallum* fragments. It proved difficult to distinguish between them. However, based on the foraging activity at these two plant species, the probability of collecting *Paspallum* fragments was estimated to be lower than 15%.

Ant and fragment masses were determined to the nearest 0.1 mg, fragment length and width to the nearest 0.5 mm. Fragment areas were calculated by multiplying the length by the mean fragment width.

The question whether ants cut dropped fragments found on the trail prior transport was addressed in a laboratory experiment. Workers from a laboratory colony of *Atta vollenweideri* were first allowed to forage at a distance of 28 metres away from the nest. This trail length was achieved in the laboratory by constructing a plastic box of 1 x 2 m with partition walls that divided the area into neighbour, 7 cm-wide trails connected successively. As a consequence, ants walking on the trail had to make a 180°-turn after 2 meters to continue walking on the next trail section. Ants were allowed to familiarise with this arrangement for several days, and there was no indication of unnatural behaviour. After this phase, workers were presented with previously-cut fragments of different length, and the probability of cutting and the lengths cut were recorded. In order to standardise the lengths of the fragments offered, rectangular fragments of large leaves of *Tilia platyphyllos* were cut with scissors and offered as “pseudo-grasses”. All fragments were in average 3.5 mm wide and either 20, 30, 40 or 50 mm long. The ants readily accepted and harvested these fragments. In each experimental series, 20 fragments of a given length were placed simultaneously at the end of the trail and the ants that initiated cutting were monitored. Ants were captured as soon as they either took an entire fragment or cut (and carried) a piece. The remaining piece of fragment was removed, so that 20 ants were measured per assay. Ant and load sizes were determined as indicated above. Four experimental series, one for each fragment length, were performed in randomised order per day. A total of 24 series were carried out over 6 days.

Results

Effect of trail sector on fragment-size determination

Since foragers of *A. vollenweideri* are highly polymorph, I compared worker size distribution in the different samples in order to detect possible differences depending on the trail sector. Ant body mass of forager cutting fragment of *C. entrerrianus* ranged from 2.5 mg to 26.9 mg, and differed significantly among groups (Kruskal-Wallis-ANOVA: $H_{(3;241)}=22.99$, $p<0.0001$). The median of forager mass averaged 9.8 mg (plant), 6.6 mg (patch), 6.6 mg (trail) and 6.9 mg (nest), respectively. Thus, cutters on the plant were significantly larger than carriers on all trail sectors (Mann-Whitney U-Test; plant vs. patch: U=907, n=51/63, $p<0.0005$; plant vs. trail: U=825.5, n=51/64, $p<0.0001$; plant vs. nest: U=1022.5, n=51/64, $p<0.001$). Conversely, there was no difference in body size among the groups on the trail (Kruskal-Wallis-Test: $H_{(2;190)}=0.51$, p=0.7, NS).

Fragment length differed significantly among groups (Fig. 1a; Kruskal-Wallis-ANOVA: $H_{(3;242)}$=45.90, p<0.0001). Fragments sampled immediately after cutting, on the plant, were significantly longer than fragments sampled at the other sectors (Mann-Whitney U-Test; plant vs. patch: U=803.5, n=51/63, p<0.0001; plant vs. trail: U=609, n=51/64, p<0.0001; plant vs. nest: U=604.5, n=51/65, p<0.0001). At the patch, fragments were of intermediate length: they were shorter than the plant fragments, but slightly longer than those collected near the nest (Mann-Whitney U-Test: patch vs. nest: U=1569, n=63/65, p<0.05). Fragment length did not correlate with ant size neither on the plant (Spearman rank correlation: r^2=0.05, t=-0.73, n=51, p=0.5, NS) nor at the patch (r^2=0.03, t=1.32, n=63, p=0.2, NS). A significant correlation was found both on the trail (r^2=0.08, t=2.93, n=64, p<0.005) and near the nest (r^2=0.22, t=4.58, n=64, p<0.0001; for linear equations see caption of Fig. 1a).

Regarding fragment width, there was no difference among the sectors with the exception of the sample taken from the trail. Fragments on the trail were slightly narrower than fragments of the plant or near the nest (Kruskal-Wallis-ANOVA: $H_{(3;242)}$=10.44, p<0.05; Mann-Whitney U-Test; plant vs. trail: U=1087.5, n=51/64, p<0.005; trail vs. nest: U=1627.5, n=64/65, p<0.05; for all other pairs p>0.05). Ant body mass correlated with fragment width in the plant and near the nest, but variation was high in all cases (Spearman rank correlation: plant: r^2=0.06 , t=2.23, n=51, p<0.05; nest: r^2=0.11 , t=3.40, n=64, p<0.005).

As for the fragment length, area of the plant fragments was significantly larger than that of all other samples (Fig. 1b; Kruskal-Wallis-ANOVA: $H_{(3;242)}$=46.58, p<0.0001; Mann-Whitney U-Test; plant vs. patch: U=757, n=51/63, p<0.0001; plant vs. trail: U=506.5, n=51/64, p<0.0001; plant vs. nest: U=772.5, n=51/65, p<0.0001). Similarly, patch fragments were shorter than plant fragments, but slightly longer than trail fragments (Mann-Whitney U-Test; patch/trail: U=1635, n=63/65, p=0.07), whereas no difference was found between trail and nest fragments. Since ant body size correlated with fragment length on the trail and at the nest, it also correlated with fragment area (trail: r^2=0.15, t=4.01, p<0.005; nest: r^2=0.37, t=7.66, n=64, p<0.0001). Note that the correlation coefficients for fragment area were much higher than for fragment length or width in the nest sample. Fragment area of plant and patch fragments did not correlate with ant mass (plant: r^2=0.10, t=1.45, n=51, p=0.15, NS; patch: r^2=0.07, t=1.20, n=63, p=0.2, NS; for linear equations see caption of Fig. 1b).

As a consequence of the differences in fragment length, width and area, fragment mass differed as well among the different sectors (Fig. 1c; Kruskal-Wallis-ANOVA: $H_{(3;241)}$=22.99, p<0.0001), with the plant fragments being significantly heavier than those of all other samples (Mann-Whitney U-Test; plant vs. patch: U=493.5, n=51/62, p<0.0001; plant vs. trail: U=156.5, n=51/63, p<0.0001; plant vs. nest: U=265.5, n=51/65, p<0.0001). Again, patch fragments were lighter than plant fragments but heavier than both trail and nest fragments (Mann-Whitney U-Test;

patch vs. trail: U=1051, n=62/63, $p<0.0001$; patch vs. nest: U=1337, n=62/65, $p<0.005$). Fragment mass correlated significantly with ant mass near the nest (nest: $r^2=0.39$, t=8.34, n=64, p<0001) and on the trail (trail: $r^2=0.12$, t=3.83, n=63, $p<0.005$), and showed a tendency at the patch ($r^2=0.18$, t=2.01, n=61, p=0.05). For the plant fragments no correlation was found (plant: $r^2=0.08$, t=1.68, n=51, p=0.1, NS; for linear equations see caption of Fig. 1c). Again, note that the correlation coefficients for fragment mass are notably higher than those for fragment length and width.

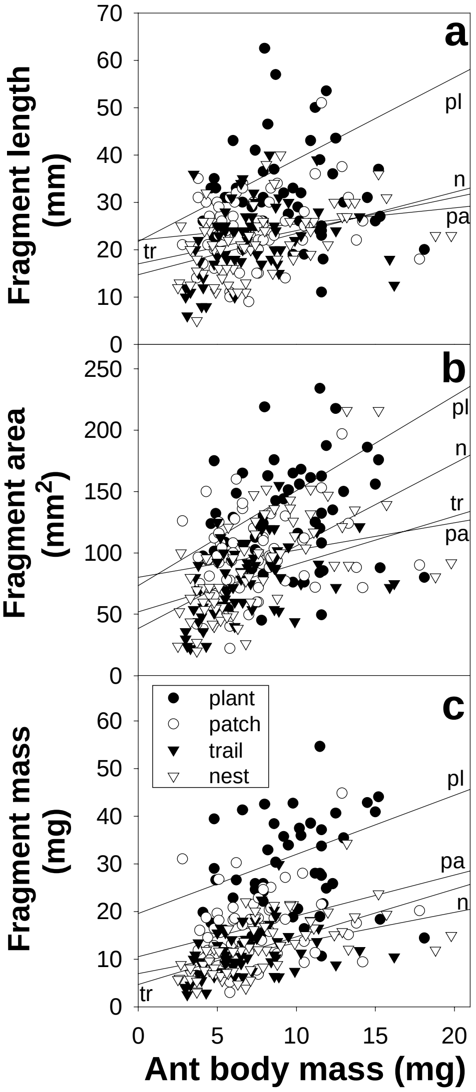


Fig. 1:
Relationships between ant size and load size for fragments of *Cyperus entrerrianus* collected either immediately after cutting (plant - pl), between plant and trail (patch - pa), on the main trail (trail - tr), or close to the nest (nest - n).

Fig 1a: Fragment length:
pl: y =1.7x+21.8, $r^2=0.05$, n=51, NS;
pa: y=0.3x+22.0, $r^2=0.03$, n=63, NS;
tr: y=0.3x+22, $r^2=0.08$, n=64, $p<0.005$;
n: y=0.9x+14.7, $r^2=0.22$, n=64, $p<0.0001$.
Fig 1b: Fragment area:
pl: y=7.7x+73.2, $r^2=0.10$, n=51, NS ;
pa: y=2.2x+80, $r^2=0.07$, n=63, NS;
tr:: y=3.9x+51.9, $r^2=0.15$, n=64, $p<0.005$;
n: y=6.7x+38.5, $r^2=0.37$, n=64, $p<0.0001$.
Fig. 1c: Fragment mass:
pl: y=1.2x+19.6, $r^2=0.08$, n=51, NS;
pa: y=0.9x+10.5, $r^2=0.18$, n=63, NS;
tr: y=0.6x+7, $r^2=0.12$, n=64, $p<0.005$;
n: y=x+4.7, $r^2=0.39$, n=64, $p<0.0001$.

<u>Effect of tissue area density</u>

Foragers transporting fragments of the soft *Leersia hexandra* ranged from 0.7 to 15.0 mg (Median=3.6 mg), and were significantly smaller than foragers transporting fragments of *Cyperus entrerrianus* (Mann-Whitney U-Test; *Cyperus* vs. *Leersia*: U=2174, n=64/189, $p<0.0001$).

Fragment length did not differ among the species considered (Fig. 2a; Mann-Whitney U-Test; *Cyperus* vs. *Leersia*: U=5331.5, n=65/190, NS). A significant correlation between fragment length and ant body mass was found both for the *Cyperus* and *Leersia* samples (Fig. 2a; *Cyperus*: r^2=0.22, t=4.58, n=64, p<0.0001; *Leersia*: r^2=0.19, t=5.31, n=190, p<0.0001; for linear equations see figure caption).

Fragments of *Cyperus* were significantly wider than those of *Leersia* (Mann-Whitney U-Test; *Cyperus* vs. *Leersia*: U=262.5, n=65/190, p<0.0001). It is important to note that most fragments of the *Leersia* sample were dry and thus were curled up, so that the original width could not be precisely determined. However, from the ant's perspective it might not matter whether the width of the load they choose to carry corresponds to a spread or a curled fragment. Correlation with ant body mass was found for both the *Cyperus* and the *Leersia* samples, but variability was high (Spearman rank correlation: *Cyperus*: r^2=0.11, t=3.40, n=64, p<0.005; *Leersia*: r^2=0.12, t=6.4, n=190, p<0.0001).

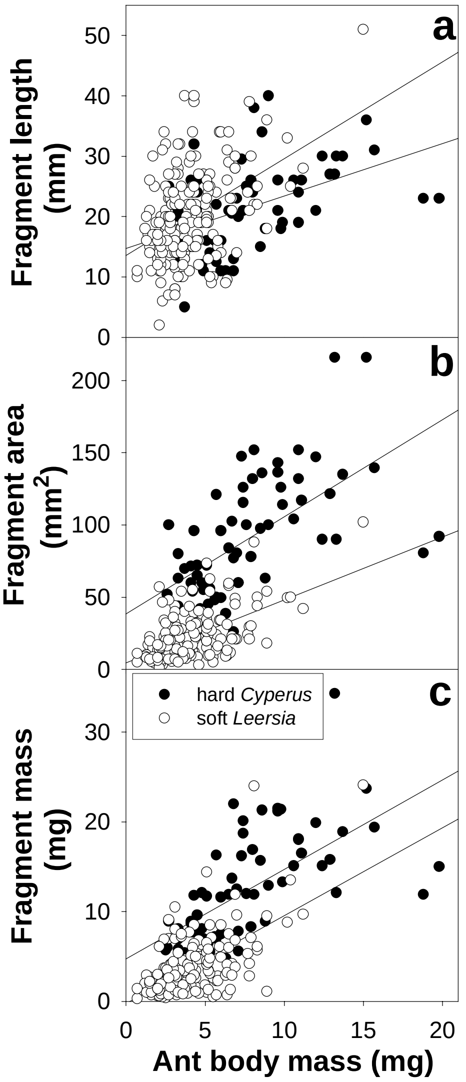


Fig. 2: Relationship between ant size and load size for fragments of the hard *Cyperus entrerrianus* fragments (closed symbols) and of the soft *Leersia hexandra* (open symbols) sampled near the nest.

Fig. 2a: Fragment length:
Cyperus: y=0.9x+14.7, r^2=0.22, n=64, p<0.0001;
Leersia: y=1.6x+13.6; r^2=0.19; n=190, p<0.0001.
Fig. 2b: Fragment area:
Cyperus: y=6.7x+38.5, r^2=0.37, n=64, p<0.0001;
Leersia: y=4.4x+4.5; r^2=0.32, n=190, p<0.0001.
Fig. 2c: Fragment mass:
Cyperus: y=x+4.7, r^2=0.39, n=64, p<0.0001,
Leersia: y=x-0.2, r^2=0.37, n=190, p<0.0001

Fragment area of *Leersia* fragments was smaller than that of *Cyperus* fragments (Fig. 2b; Mann-Whitney U-Test; *Cyperus* vs. *Leersia*: U=505.5, n=65/190, p<0.0001). Since ant body mass correlated with both fragment length and width, it also correlated with fragment area (*Cyperus*: r^2=0.37, t=7.66, n=64, p<0.0001; *Leersia*: r^2=0.32, t=8.02, n=190, p<0.0001; for linear equations see caption of Fig. 2b). Note that the correlation coefficients are much higher than the coefficients for load length or width.

Fragments of *Leersia* were significantly lighter than that those of *Cyperus* (Fig. 2c; Mann-Whitney U-Test; *Cyperus* vs. *Leersia*: U=893, n=65/189, p<0.0001). Fragment mass correlated significantly with ant mass for both samples (*Cyperus*: r^2=0.39, t=8.34, n=65, p<0001; *Leersia*: r^2=0.37, t=8.21, n=190, p<0.0001; for linear equations see figure caption). Again, correlation coefficients for fragment mass were higher than the coefficients for fragment length and width.

Are fragments cut again on the trail?

In order to investigate whether ants cut fragments found on the trail prior transport, workers from a laboratory colony of *A. vollenweideri* were presented with previously cut fragments of different length, and the probability of cutting and the lengths cut were recorded. The probability to cut a fragment increased with increasing initial length: Only 21% of the 20mm-fragments were cut, whereas 62% of the 30mm, 83% of the 40mm and 97% of the 50mm-fragments were cut prior to transport (Fig. 3). Forager size ranged from 2.0 to 12.6 mg (Median 5.0 mg), and it did not differ among ants cutting pieces out of fragments with different initial lengths (Kruskal-Wallis-ANOVA: $H_{(3,459)}$=3.154, p=0.4, NS).

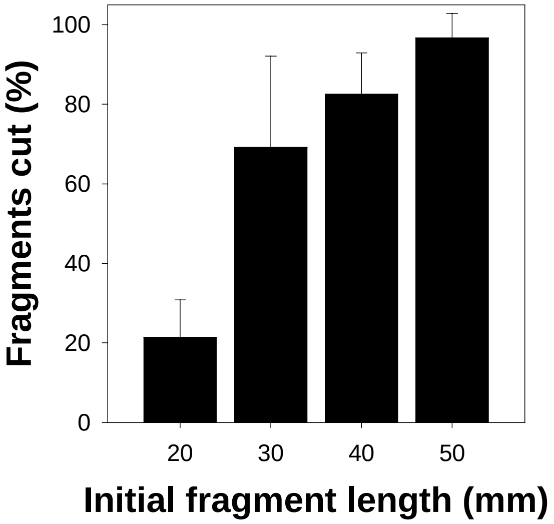


Fig. 3:
Frequency of fragments of *Tilia platyphyllos* with different initial lengths which were cut prior to transport.

For those fragments that were cut prior to transport, the absolute lengths cut by the ants significantly differed among groups, with exception of 40 and 50 mm initial length (Fig. 4a; Kruskal-Wallis-ANOVA: $H_{(3,326)}=81.17$, $p<0.0001$; Mann-Whitney U-Test; 20 vs. 30 mm: $U=689.5$, $p<0.0005$; 30 vs. 40 mm: $U=2178$, $p<0.0001$; 40 vs. 50 mm: $U=5335$, $p=0.5$, NS). Interestingly, if one compares the length of the fragments cut *relative* to the initial length, i.e., the relative length as a percentage, there was no difference among the groups with the exception of the 50mm-fragments (Fig. 4b; Kruskal-Wallis-ANOVA for all fragments: $H_{(3,326)}=25.00$, $p<0.0001$; for 20, 30 and 40 mm fragments: $H_{(2,211)}=3.14$, $p=0.2$, NS; Mann-Whitney U-Test: 40 vs. 50 mm: $U=3957$, $p<0.0005$). Thus, up to a length of 40 mm, which corresponds to the longest fragments observed to be carried in the field (see Figs 1 and 2), the absolute length cut increased with increasing initial length of the fragment, whereas the relative length remained constant and averaged 50% of the total length. In other words, fragments were cut in two similarly long portions. Because of the differences in initial length, the largest pieces cut averaged 23 mm in length. For the largest fragments, i.e., fragments with initial length of 50 mm, workers selected a length not larger than 23 mm to cut, so that the absolute length was similar to that of the 40mm-group, and the relative length shorter.

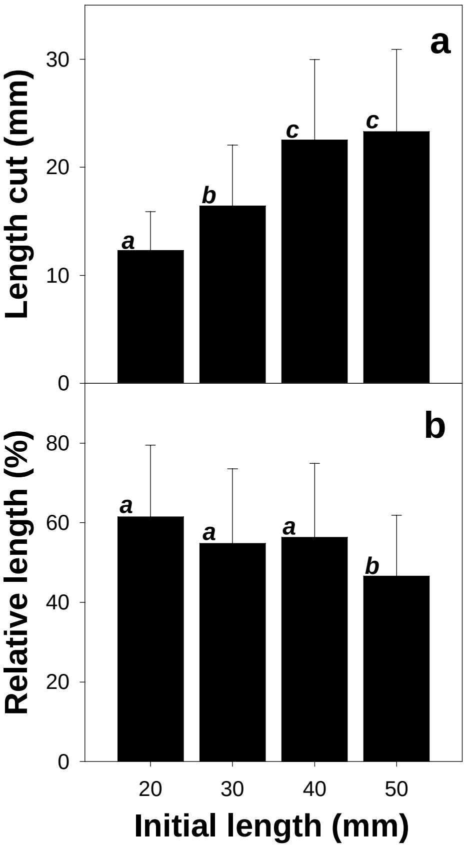


Fig. 4:
Fragment lengths cut by workers out of fragments of *Tilia platyphyllos* of different lengths. Columns sharing the same letters are not statistical different (Kruskal-Wallis-ANOVA and Mann-Whitney-U-Test $p<0.05$, n=6 series).

Fig. 4a:
Absolute lengths cut by the workers.
Fig. 4b:
Relative length cut, i.e. percentage of length cut relative to the initial length.

As forager size did not differ among groups, data were pooled for regression analyses. Ant mass correlated significantly with fragment length, though with a low correlation coefficient

($y=16.9+0.7x$, $r^2=0.02$, $n=309$, $p<0.01$). Consequently, as fragment width was held constant, ant mass also correlated with fragment mass ($y=6.5+0.4x$, $r^2=0.04$, $n=309$, $p<0.0001$), indicating that larger ants cut longer, heavier fragments.

Discussion

I investigated fragment-size determination and size-matching in the grass-cutting ant *Atta vollenweideri* as a function of the distance from the nest. Comparison of forager size on different trail sectors showed that cutting ants were significantly larger than carrying ants, thus indicating that they represent specialised groups. Because of body size allometry, large ants have proportionally bigger heads and therefore larger mandibular muscles, which averages one fourth of the total body mass (Roces and Lighton 1995). Cutting was shown to be an energetically extremely intensive behaviour, with metabolic rates being about 30 times higher than those observed during resting (Roces and Lighton 1995). During walking, metabolic rates are approximately seven times higher than during resting (Lighton *et al*. 1987; Roces and Lighton 1995). Carrying requires therefore less energy per unit time, but it might demand a considerable time investment, since single ants may need several hours for a single foraging trip (Lewis *et al*. 1974). Under such conditions, it appears advantageous for a colony to have size-related division of labour, with larger workers performing the energetically most demanding task, and smaller engaged in the time-consuming tasks. In fact, cutting workers of *A. vollenweideri* are frequently observed dropping or passing their fragments to nestmates, with small workers transporting them to the nest (Chapter 4).

The size of freshly cut fragments correlated with the size of the cutters only regarding fragment width, but not length, area or mass. With regard to the division of labour, it seems conceivable that cutters do not adjust fragment length or mass to their body size, as they will not carry the fragments back to the nest. The only parameter that appears to be relevant for their foraging performance is the fragment width, as cutting is a very energy-demanding task, and a colony might benefit in having larger workers cutting at wider grass blades. This indeed was the case in our measurements, although variability was very high. Hence, grass width may be only one of the relevant variables used by foragers to decide what grass blade should be cut.

Fragment-size determination was clearly dependent of the distance from the nest. Fragments collected immediately after cutting were shown to be larger than those sampled subsequently on the trail. As a consequence, fragments must have been cut a second time. I frequently observed long, freshly cut fragments dropped on the ground beside the plant, with ants cutting them once more. In addition, our laboratory experiment also showed that long fragments found on the trail were indeed cut once more. Interestingly, the size of the fragment sampled in the field between the plant and the trail were of intermediate length, shorter than those harvested on the plant, but longer than those on the trail or near the nest. This suggests that some fragments were cut, but only after being transported a short distance to the main trail. One might argue that some cutters, instead of dropping their fragments, might have carried them directly to the main trail, yet patch ants were in average smaller than cutting ants, thus contradicting this idea. Rather, it seems that some patch carriers chose fragments that they either cut after having reached the main trail, or put the fragments down again, so that other workers subsequently cut them.

A similar two-stage foraging mode was described for the leaf-cutting ants *Atta sexdens* (Fowler and Robinson 1979) and *Atta cephalotes* (Hubbell *et al*. 1980). A group of arboreal cutters severs leaves at their stems, another group of foragers cuts these dropped leaves on the ground into semicircular fragments that are deposited on the main trail, and finally other foragers carry the fragments to the nest. It is tempting to speculate about the occurrence of a similar modality in grass-cutting ants, with a group of large workers cutting the grass plants, a second group of smaller "short-distance carriers" that often cut the fragments again before transporting them until the main trail, and a group of "long-distance carriers" that carried the fragments to the nest.

If such foraging modality occurs, one would not necessarily expect any size-matching between ants and loads neither for cutters (as mentioned above), nor for "short-distance carriers", which carry fragments for a very short distance from the plant to the patch. This is exactly what I found in the field. The extent of size-matching was observed to increase during the transport along the trail, a phenomenon similar to what Reyes-López & Fernández-Haeger (2001) reported for the seed-harvester ant *Messor barbarus*. This strongly indicates that a second cutting event or a transfer of loads to nestmates of different size occurred, either directly or indirectly by putting the fragment on the trail. I frequently observed dropped fragments remaining briefly on the main trail that were then collected by other foragers and transported to the nest.

Near the nest, a strong correlation between ant size and load size was found for both the hard *Cyperus* and the soft *Leersia* fragments, in all measured variables. However, correlation coefficients for fragment mass and fragment area were much higher than for fragment length or width, suggesting that these variables are biologically more relevant than the others. These differences in size-matching as a function of fragment mass and length probably result from the selectivity of workers along the trail when collecting dropped fragments for transport: Workers appear to respond to the difficulties in manoeuvring a piece when trying to lift it, so that fragment mass may directly affect their decisions. Size-matching is expected to be particularly relevant for long-distance carriers, since load mass strongly affects transport efficiency by influencing walking speed and therefore material transport rate (Röschard and Roces 2002c; Rudolph and Loudon 1986). This view is further supported by the comparison of the worker size distribution between the two plant species having different tissue area density. For a given area, loads with higher tissue area density will be heavier than those with lower area density. Foragers carrying fragments of the soft *Leersia* were much smaller than those carrying *Cyperus* fragments.

Remarkably, load length was held approximately constant, irrespective of the large differences in tissue toughness. 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 between 45 and 90° with the ant body axis. Workers have severe difficulties in balancing long fragments, and I recently experimentally showed that fragment length poses a constraint to the economics of transport: independent of their mass, long fragments are transported significantly slower than shorter, so that material intake rate is reduced (Röschard and Roces 2002c; Chapter 3). Short fragments, on the other hand, are transported at a faster pace, but material intake rates may be low. Ants are therefore expected to be very selective with regard to the fragment lengths they cut. The range of "appropriate" lengths seems to be restricted to maximal values of 40 mm.

The lengths of the fragments cut in the laboratory corresponded with the range observed in the field. This gives further support to the idea mentioned above that ants chose fragments within a certain length range. When finding dropped fragments on the ground, ants may decide to cut a given length after having assessed the difficulties in transporting the complete fragment, for instance after trying to lift it. Interestingly, single ants were frequently observed to walk along the dropped fragment and to steadily bite into it, a "testing" behaviour that was regularly observed in the field when workers climb on a grass blade before cutting. Our laboratory experiments showed that workers might have assessed the total length of the dropped fragments in order to cut them into halves, thus selecting a *relative* length to initiate a cut. In addition, workers cut pieces of an *absolute* length when the dropped fragments were particularly long. Taken together, these findings indicate that workers make specific decisions when cutting dropped fragments, but the measures used to determine the length of the piece to be cut depend on the assessment of the total fragment length. And as discussed above, fragment-size determination also depends on the distance from the nest. The mechanisms involved in load-size determination by grass-cutting ants are completely unknown, and experiments focusing on them are already under way.

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

Summary. In the present study I 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 two-fold 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 was observed to be higher when they carried short fragments: A two-fold 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 lower pace. For the sizes tested, heavy fragments yielded a higher transport rate in spite of the lower 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 energetic of cutting, workers might maximise 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 maximising harvesting rate at the cutting site and minimising the effects of fragment size on material transport rates.

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 meters 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; Wetterer

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 energetic 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 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 a worker 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 has 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; Burd 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; Jonkman 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 the grass width, which usually does not differ very much along the blade except at its tip. Hence, cutting a larger (longer) fragment does neither imply 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 (Daguerre 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 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 gravitational centre. 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, I 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. I first measured the length of natural grass fragments cut by workers in field colonies. I 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 two-fold 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 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 *Atta vollenweideri* in the Biological Station “El Bagual” in Formosa, North Argentina, from October to December 1999. In order to quantify the fragment sizes harvested naturally by the ants, I collected 33 foragers randomly during four consecutive days with their loads shortly after they had finished cutting their fragments out of the sedge *Cyperus entrerrianus* (Cyperaceae). The natural trail was 10m 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. The fragments were cut out of standard paper ($80 g/m^2$), soaked with orange juice for at least one hour, and then dried. Based on the measurements of the plant fragments naturally cut, I 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 of the sticking, those fragments were slightly, but not significantly, heavier than the long ones (mass range: 16-19 mg; t-test for independent samples: $n_{(double)}=61$, $n_{(long)}=64$, $p>0.05$).

Fragments were placed on an active trail. I presented them alternating between the three types and measured the running speed of the first 10 laden workers running back to the nest on a 50 cm trail sector. Laden foragers were then caught and weighed. 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, ambient temperature varied between 18.2 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 that, workers from a laboratory colony of *A. vollenweideri* were allowed to forage in an arena of approx. 1m x 0.5m connected to the nest by a 1.5m 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 between 16-18 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, I 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 to 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 between 8-9 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 thirty fragments. Care was taken that fragments were not lying 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 twenty replicates was performed.

Results

Lengths of grass fragments cut

The distribution of lengths of natural grass fragments cut by the ants in the field is shown in Fig. 1. Fragments ranged from 12 to 49 mm, with most fragments being 20 to 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 to 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).

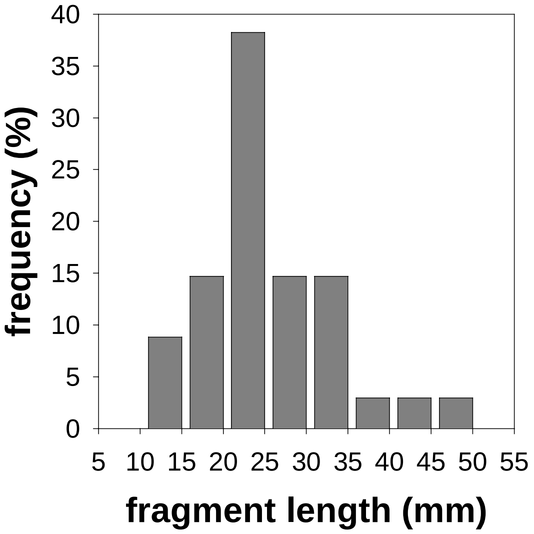


Fig. 1: Frequency distribution of lengths of grass fragments (*Cyperus entrerrianus*) naturally cut by ants in the field (n=33). Numbers on the X-axis indicate the upper limit of the respective range, with the limit being included.

Body mass of workers carrying the grass fragments varied from 5.8 to 23.1 mg (average 12.0 ± 3.8 mg, n=33). 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 correlation 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 and 2b). The three regression lines differ significantly from each other with the short (and lightest) fragments being carried fastest (ANCOVA for short and double fragments: equal slopes but different intercepts: a) field: $F_{(1,123)}$=13.55, p<0.005; b) lab: $F_{(1,102)}$=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: a) field: $F_{(1,122)}$=61.29, p<0.0001, b) lab: $F_{(1,100)}$=88.96, p<0.0001).

The differences in speed observed between short and double fragments are much smaller than those between 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 two-fold increase in mass. For the same mass, longer fragments were carried slower. This was observed in both field and laboratory experiments.

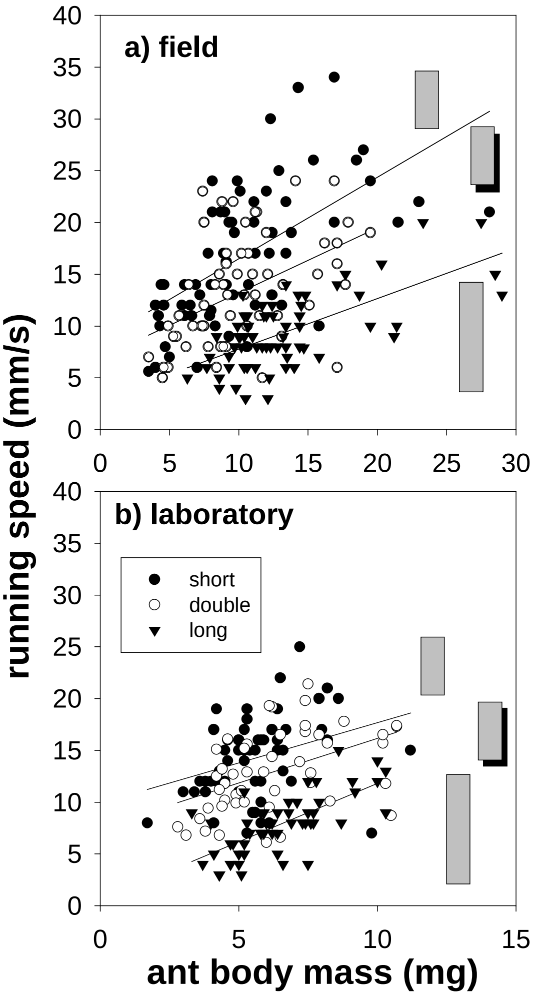


Fig. 2:
Running speed of foragers carrying an orange-treated paper fragment.

Fig. 2a: field colony:
short fragments: y=8.54+0.79x, r²=0.36, n=65, p<0.0001;
double fragments: y=6.72+0.65x, r²=0.23, n=61, p<0.001;
long fragments: y=3.11+0.47x, r²=0.41, n=64, p<0001.
Fig. 2b: laboratory colony:
short fragments: y=10.18+0.74x, r²=0.09, n=56, p<0.05;
double fragments: y=7.56+0.86x, r²=0.22, n=49, p<0.001;
long fragments: y=0.49+1.14x, r²=0.47, n=54, p<0001.

Note differences in scale on the X-axis between Fig. 2a and 2b. The shaded boxes symbolise the three different fragment types used during the 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 characterise more properly the foraging performance at the colony level, since it represents a measure of the amount of material being transported to the colony a given distance per unit time (Lutz 1929). The results of field and laboratory experiments are shown in Fig. 3a and 3b, 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: a) field: $F_{(1,123)}$=33.88, p<0.0001; b) lab: $F_{(1,102)}$=59.09, p<0.0001). This indicates that in the range tested, the increase of material achieved by 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: a) field: $F_{(1,122)}$=89.77, p<0.0001, lab:, b) $F_{(1,100)}$=75.88, p<0.0001), because of the lower 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).

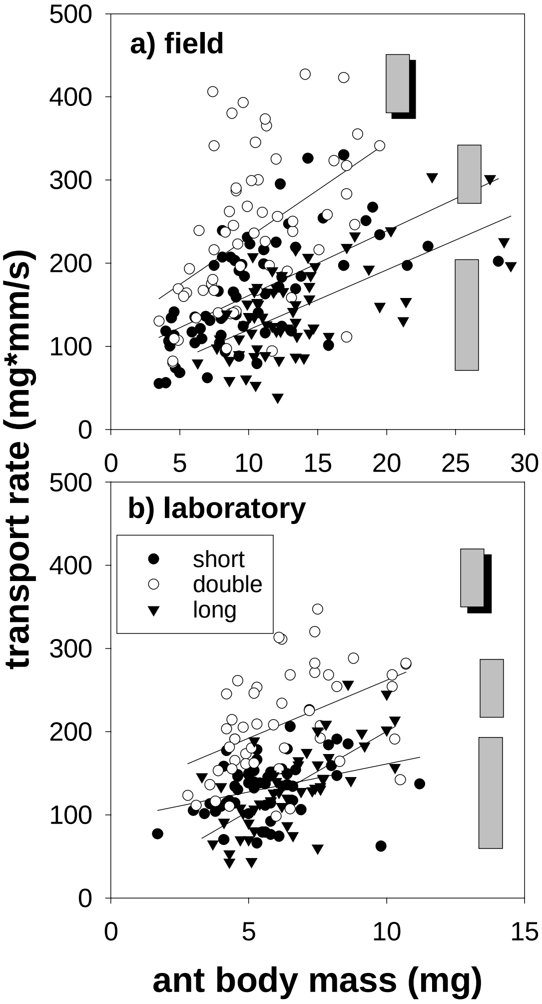


Fig. 3: Gross transport rate of foragers carrying an orange-treated paper fragment.

Fig. 3a: 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.
Fig. 3b: 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 Fig. 3a and 3b. 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, see caption). 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).

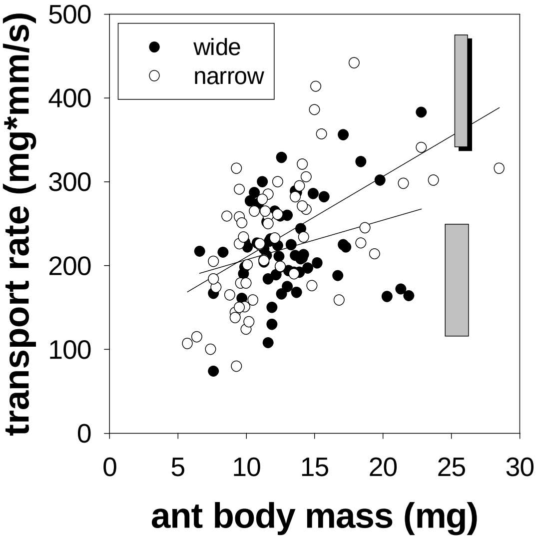


Fig. 4:
Gross transport rate of foragers carrying fragments of different width (field measurements). Narrow fragments $y=113.87+9.63x$, $r^2=0.30$, $n=60$, $p<0.0001$; wide fragments: $y=159.99+4.71x$, $r^2=0.08$, $n=60$, $p<0.05$. The shaded boxes symbolise the two different fragment types used during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

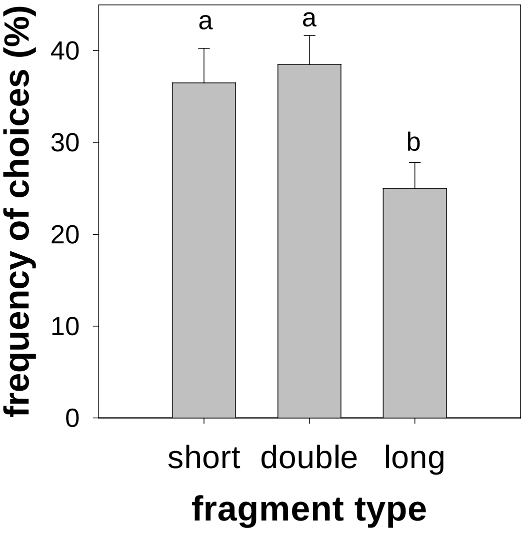


Fig. 5:
Load size preference of foragers in the field. The Y-axis shows the mean percentage of choices ± SE (n=20 experimental series). Bars sharing the same letter are not significantly different (One-Way ANOVA).

Fragment-size preference

Double fragments were chosen significantly more often than long fragments, despite of their equal mass (Fig. 5). In addition, workers selected more often short 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 (Newman-Keuls-comparison: p=0.7, NS).

Discussion

I 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 lower 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 serious decline in transport speed. This indicates that length reduced manoeuvrability of the fragments during transport, presumably by displacing the gravitational centre of the laden workers. In fact, I 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 lab 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 by holding them more or less vertical overhead in a balanced position, an increase in fragment area is unlikely to cause a marked displacement of the gravitational centre during transport. Rudolph and Loudon (1986) showed that an experimental increase of 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 hypothesised 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 avoid parasitic attacks (Feener 1990). In the field, I 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 to 30 minutes 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 energetic is considered, the longer a grass fragment, the larger the amount of material harvested per unit cutting effort. This is the consequence that cutting length, i.e., grass width, remains more or less invariant 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 maximising individual harvesting rate per unit effort during cutting, and minimising 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 cannot 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 the cut to compensate for experimental changes in fragment weight during the process of cutting, i.e., workers do not directly assess 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 (lengthy) 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.

Cutters, carriers and bucket brigades - Distance-dependent foraging strategies in the grass-cutting ant *Atta vollenweideri*

Summary. Grass-cutting ants, *Atta vollenweideri*, harvest grass fragments that serve as substrate for the cultivation of a symbiotic fungus. Fragments are transported to the nest for considerable distances along well-established trunk trails. I investigated task partitioning during foraging by recording the behaviour of marked ants while cutting, and by monitoring the transport of fragments from the cutting until they reached the nest. *A. vollenweideri* foragers showed division of labour between cutting and carrying, with larger workers cutting the fragments, and smaller transporting them. This division was absent for food sources very close to the nest, when no physical trail was present. Along the trail, the transport of fragment was a partitioned task, i.e., workers formed bucket brigades composed of 2 to 5 carriers. This sequential load transport occurred more often on long than on short trails. The first carriers of a bucket brigade covered only short distances before dropping their fragments, and usually turned back and walked to the patch. The last carriers covered the longest distance. The probability of dropping the carried fragment on the trail was independent of both worker and fragment size, and there was no particular location on the trail for dropping, i.e., fragments were not cached. Transport time was longer for fragments transported *via* a bucket brigade than for those transported by single workers all the way to the nest. Thus, transport by a bucket brigade did not save foraging time. Two hypotheses concerning the adaptive value of bucket brigades are discussed. It is suggested that rather than increasing the gross transport rate of material, the transport via bucket brigades may enhance the flow of information about the resources being harvested, thus leading to a quicker build-up of workers at the harvesting place.

Introduction

Social insects have developed a variety of strategies for food retrieval that often involve a high degree of co-operation and co-ordination. In many species, prey items that a lone worker could not manage are retrieved co-operatively (Anderson and Jadin 2001), so as to increase transport speed by forming special transport groups (Franks 1989), or to effectively defend the food items against competitors (Traniello and Beshers 1991).

In addition to these simultaneously co-ordinated actions, workers of some ant species show a sequential co-operation in which a food item or building material is passed consecutively from one worker to the next, over the length of the route from the source to the final destination in the nest. Sequential co-operation may lead to a decreased energy and time investment during foraging (Jeanne 1986b; Reyes-López and Fernández Haeger 1999), with a concomitant reduction in foraging risks (Jeanne 1986b). Sequential co-operation may be regulated by negative feedback, for instance by delays that occur when a worker has to wait until it can pass over its load to a nestmate (Seeley 1989b).

A sequential transport of collected material facilitates the occurrence of a high degree of specialisation and task partitioning in the colony. Task partitioning can be defined as a process in which *one* task is split up between different worker groups, in contrast to division of labour in which *different* tasks are performed by different worker groups, e.g. guarding and brood caring (Oster and Wilson 1979; reviewed in Ratnieks and Anderson 1999). Leaf-cutting ants of the tribe Attini show both division of labour (Weber 1972; Wilson 1983a) and task partitioning to an extraordinary extent, including different contexts such as foraging (Fowler and Robinson 1979; Hart and Ratnieks 2000a; Hubbell *et al*. 1980), trail construction (Howard 2001), or waste management (Anderson and Ratnieks 2000; Hart and Ratnieks 2001).

Sequential co-operation and task partitioning during foraging were described for the leaf-cutting ants *Atta sexdens rubropilosa* and *A. cephalotes* at the beginning of a foraging process (Fowler and Robinson 1979; Hubbell *et al*. 1980). A group of arboreal cutters cuts large quantities of leaves and drops them to the ground. Workers of a second forager group cut small pieces out of these leaves and transport them to the main trail. Fragments are dropped on the trail or transferred directly to “carriers” that transport them to the nest. Thus, ants form a transport chain or bucket brigade in which the foraging process is split up into several stages. Workers in these functional groups seem to be specialised as body size differs among them, and arboreal cutters were not seen to carry fragments back to the nest. During transport, task partitioning was also recently reported in *A. colombica*, with fragments being directly transferred or cached on the trail in 21% of the cases (Anderson and Jadin 2001).

Foraging by grass-cutting Attini ants might be a particularly well-suited system for studying task partitioning and sequential load transport because ants harvest grass fragments (Jonkman 1976) and therefore the whole harvesting process from the source to the nest can be directly monitored and experimentally manipulated. Preliminary observations on *Atta vollenweideri* indicated that cutting ants usually drop their grass fragments near the harvested plant, and that both load dropping and load transfers occur along the trail. The aim of the present study was to investigate division of labour, task partitioning and the occurrence of bucket brigades in foraging grass-cutting ants, *Atta vollenweideri*. In the field, size-related division of labour was addressed by measuring body size of cutting and carrying workers. The occurrence of sequential transport of grass fragments, i.e. of bucket brigades, was quantified by following marked grass fragments all their way to the nest and by recording the number of transfers between carriers, the distances covered by each one, and their body size. Experiments were performed on trails of different length in order to elucidate the effect of foraging distance on the occurrence of bucket brigades.

Material and Methods

Ethograms of cutters

Experiments were performed in the National Park Río Pilcomayo in Formosa province, North Argentina, between November 1998 and May 1999. In order to investigate cutting behaviour and task partitioning between cutting and carrying ants, 22 ants were marked with a small dot of Edding® paint marker 780 or liquid TippEx® while they were cutting fragments out of the grass *Paspallum intermedium* (Poaceae). They were subsequently followed for at least 45 minutes or until they entered the nest, with the exception of two ants that were lost after 25 and 30 minutes of observation, respectively. The behavioural responses of the ants after cutting, either dropping the fragment or carrying it towards the nest, was noted, and both the time and the distance they carried their loads were recorded. As most ants cut one or maximally two fragments during the observation time, data for a total of 37 cutting events were recorded.

In order to have a restricted foraging area that makes observations of single foraging workers possible, a circular area of ca. 1.5m in diameter was defined at a distance of 5m from the nest, beside an existing trail of 35m total length. A plastic fence of approx. 40cm height treated with plant oil, in order to avoid escape of the ants, surrounded the 5m trail sector and the foraging area. The original trail was connected with the enclosed sector by wooden bridges, so as to regulate the number of foragers collecting outside or inside the arena during observations. The area was completely cleared and only few grass plants of *P. intermedium* were transplanted about half a day before an experimental series, in order to standardise the plants provided each experimental day and to maintain foraging distance constant.

In addition, foragers from a second colony were observed while harvesting a *P. intermedium* plant growing at 0.5m from the nest entrance. Cutting and transport of 15 fragments was observed. Ant body size was determined in both experiments as the maximal head width to the nearest 0.25 mm by visually comparing the monitored ant with a template with fixed ants of different sizes.

„Fragmentograms“

To investigate the whole process of cutting and transport, newly cut grass fragments were marked with a small dot of Edding® paint marker 780 or liquid TippEx®, and followed until they reached the nest. Since observations were centred on the fragments, the set of data obtained for a given fragment was termed „fragmentogram“, i.e., the time intervals and the distances a given fragment was carried by sequential foragers were noted, as well as the „waiting times“, i.e. the time a fragment was left on the trail before being retrieved by another worker. Foragers involved in the sequential transport were caught immediately after transferring or dropping the fragment, and weighed to the nearest 0.1 mg. Marked fragments, together with the carriers, were collected at the nest entrance and weighed as indicated above. Fragment length and width were determined to the nearest 0.5mm.

Since plants naturally harvested by the ants may differ in quality and attractiveness, ants were presented with a standardised source of artificial “paper plants”. They were produced by soaking paper stripes of 15cm length and 3.5 mm width in diluted orange juice (50% juice in water), and by drying them afterwards. Ten to 15 paper stripes were put into a small plastic vial that was “planted” on the ground between a plant actually harvested and the main trail, 10 to 20cm beside the trail. Two active trails of different length of a large field colony were chosen for the experiments, where ants were actively cutting fragments out of the sedge *Cyperus entrerrianus* (Cyperaceae). One trail was 10m (henceforth: “short trail”), and the other 28m long (henceforth: “long trail”). Paper plants were presented at one location at the time.

In order to control for a possible experimental artefact due to the use of artificial paper plants, a total of 36 “fragmentograms” were also recorded for natural fragments cut by workers out of *Cyperus entrerrianus* at 10m from the nest. Before foraging activity started, the grass blades were treated with the diluted orange juice, so as to increase their attractiveness.

Results

The behaviour of cutters as a function of distance

Cutters were only seldom involved in the transport of fragments. When cutting fragments out of *Paspallum intermedium* at 5m from the nest, they either directly dropped most of their fragments, or carried them only until the base of the plant (78%, 29 out of 37 fragments). Sixteen percent of the fragments (6 fragments) were dropped on or near the main trail. Cutters dropped their loads, i.e., no direct fragment transfers to other workers were observed. Only 5% of the fragments (2 fragments) were carried to the nest by the cutters (Fig 1).

The behaviour of the cutters depended on the distance between the food source and the nest. If the harvested plant was located at 0.5m from the nest entrance, 60% of a total of 15 fragments were carried directly by the cutters to the nest. Forty percent of the fragments were dropped. The differences between the two distances are statistically significant (Fig. 1, Chi-square test, Yates-corrected, dropping vs. carrying; 5m: $\chi^2=5.51$, $p<0.05$; 0.5m: $\chi^2=15.94$, $p<0.0005$).

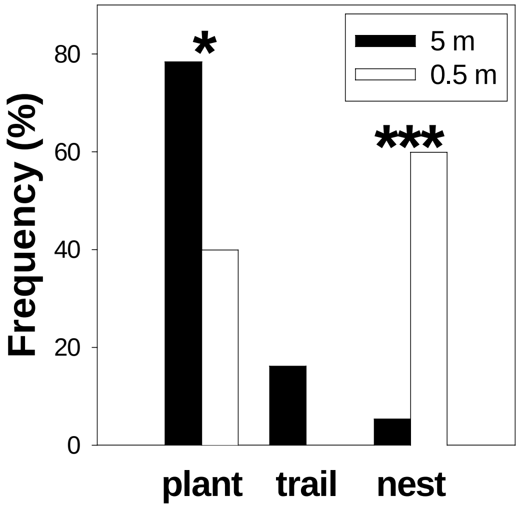


Fig. 1:
Behaviour of foragers after cutting a fragment as a function of the distance from the nest. Cutters either dropped their fragments immediately after cutting ("plant"), carried them to the main trail ("trail"), or to the nest. The harvested plants were located either at 5m from the nest (black bars) or directly at 0.5m from the nest entrance (white bars). Body size of observed ants ranged from 1.5 to 3.0mm head width.

At 5m from the nest, cutters were observed to spend a considerable time searching for cutting sites or walking on the ground. While walking on the ground, workers occasionally picked up a dropped fragment and carried it towards the nest. Usually cutters dropped those fragments after a short distance when reaching the main trail. Thus, irrespective of whether cutters carried their own or foreign, fragments were usually transported until the main trail and rarely to the nest. Transport times by the cutters ranged from 25s to 5min for own, and from 10s to 12min for foreign fragments before they were dropped or the cutter reached the nest. However, longer carrying times do not necessarily indicate a longer carrying distance, as loaded ants often kept walking back and forth the same section of the patch or the trail, probably reinforcing the trail with pheromones.

As observed when cutting plant fragments, workers cutting fragments out of the paper plants were only seldom involved in transport, but dropped or carried the pieces only a short distance: 51% and 31% of the fragments were dropped at distances of 10 and 28m, respectively (n=27 for the short trail; n=32 for the long trail). Cutters carried their fragments for less than one meter in 3% (short trail) and 26% (long trail) of the cases, i.e., fragments were laid down shortly after reaching the main trail. Thirty-two percent (short trail) and 8% (long trail) of the cutters performed the complete transport until the nest.

Figure 2 presents data on the distances covered by the loaded cutters, on both the short and long trail. Foraging distance did not influence the frequency of dropping a fragment directly after cutting (Chi-Square-Test: $\chi^2=0.37$, $p=0.5$). However, the probability that a cutter carried its fragment to the nest depended on distance: Significantly more cutters reached the nest with their fragments on the short than on the long trail (Chi-Square-Test: $\chi^2=7.34$, $p<0.01$). For those dropped fragments, there was no particular location along the trail for dropping (Fig. 2), i.e., cutters did not cache the fragments.

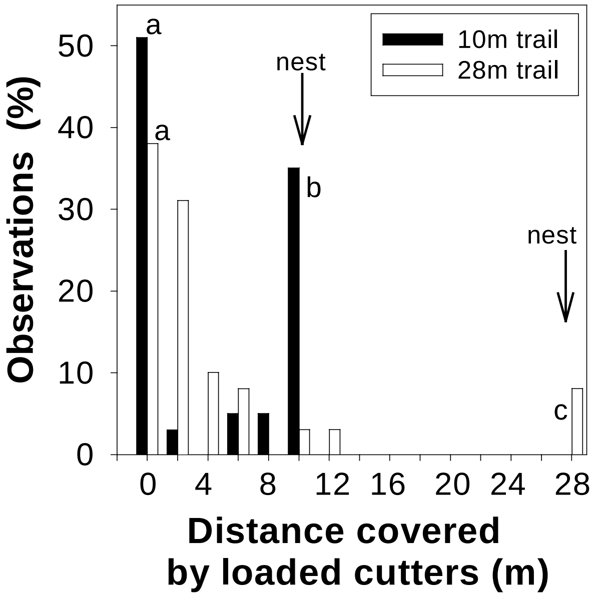


Fig. 2:
Transport distance covered by cutters after cutting a fragment out of a “paper plant”, at two different distances from the nest. Bars at “0m” indicate that fragments were dropped immediately after cutting. The black bar at 10m and the white bar at 28m show the number of fragment cutters carried directly to the nest. Trails differed in the frequency of cutters reaching the nest (bars marked with “b” and “c”) but not in the frequency of immediate dropping (bars marked with “a”).

The question arises whether body or load size were responsible for the cutter’s decision to drop a load. Based on the number of data, different statistical analyses were used for the short and the long trail. For the short trail, average body and load sizes of cutters that transported their fragments to the nest (“carry”) were compared with those of workers that dropped their fragments after cutting (“drop”). For the long trail, the relationship between carrying distance and either body or load size was analysed. It is important to indicate that during transport, workers of *A. vollenweideri* take the fragments with their mandibles at one end and carry then in a more or less vertical position, usually inclined backward forming an angle between 45 and 90° with the ant body axis. Load length affects significantly maneuverability and transport speed, because of the marked displacement of the center of gravity (Röschard and Roces 2002c; Chapter 3). Therefore, load size was analysed as both load mass and load length.

Ant body mass did not differ significantly between load-carrying and load-dropping cutters on the short trail (Median, Quartile range; “carry”: 12.2 mg, 5.05, n=12; “drop”: 13.5 mg, 7.5, n=14; Mann-Whitney-U-Test: U=74.0, Z=0.51, p=0.6, NS). Neither differed load mass nor load length (load mass, “carry”: 11.7 mg, 6.05, n=12; “drop”: 9.9 mg, 5.6, n=19; U=103, Z=-0.45, p=0.7, NS; load length, “carry”: 27.5 mg, 10.5, n=12; “drop”: 28.5 mg, 7.0, n=18; U=84.0, Z=1.02, p=0.3, NS). Similarly, there was neither a significant relationship between transport distance of the cutter and its body mass on the long trail (y=16.5-0.58x, r=-0.23, n=21, p=0.3, NS), nor load mass (y=7.29+0.64x, r=0.39, n=22, p=0.08, NS), nor load length (y=21.5+0.82x, r=0.28, n=22, p=0.2, NS). Hence, neither ant size nor load size caused the cutter to drop their fragment.

When compared with carrying workers, cutters were significantly larger than carriers on both the short and the long trail (short trail: Median, Quartile range; cutters: 13.4 mg, 6.65, n=32; carriers: 9.2 mg, 5.55, n=32; U=311.5, Z=2.69, p<0.01; long trail; cutters: 13.4 mg, 7.4, n=35; carriers: 8.9 mg, 5.1, n=72; U=412, Z=5.63, p<0.0001). Carriers were those ants that picked up and carried a fragment they did not cut, irrespective of their position along a sequential line of transport (see below).

Task partitioning: bucket brigades

Three different modalities for the transport of fragments along the trail were observed. First, the cutter carries the fragment directly to the nest, as described above. Second, fragments put down by the carriers on the trail, or transferred directly, are retrieved by a worker and carried all the way to the nest. Such workers were called “single carriers”. Third, fragments found on the trail or directly received from nestmates are transported consecutively by different carriers via a “bucket brigade”. Following our definition of “carriers”, a bucket brigade with 2 carriers implies that a total of 3 ants are involved (cutter plus 2 carriers).

When harvesting the artificial paper plants, bucket brigades were often observed along both the short and the long trail. The frequency of occurrence of bucket brigades significantly depended on trail distance. On the long trail, 55% of the fragments were transported by bucket brigades, whereas the frequency on the short trail was only 16% (Fig. 3; Chi-Square test: χ^2=13.11, p<0.0005). Fifty percent of the bucket brigades were composed by 2 carriers, 32% by 3 carriers, and 4 or 5 carriers occurred in 18% of the cases. Regarding the other transport modalities, cutters transported the fragments to the nest significantly more often on the short than on the long trail (Fig. 3). The frequency of fragments transported by single carriers, conversely, was independent of foraging distance, averaging 53% and 38% on the short and long trail, respectively (Fig. 3).

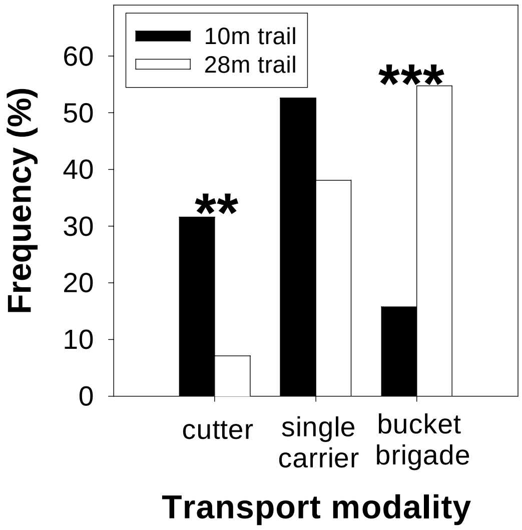


Fig. 3:
Modality of load transport as a function of foraging distance. On the long trail, significant more bucket brigades occurred than on the short trail.

With regard to the mode of leaf transfer, it is important to indicate that only 12.5% and 11.5% of the fragments were transferred directly on the short and long trail, respectively, i.e., most fragments were dropped on the ground and collected by outgoing workers that then turned back and returned to the nest. When not directly transferred, fragments were dropped in the middle of the trail. Ants neither prefer certain places on the trail for dropping fragments, nor did they build up piles at a given location. Dropped fragments attracted unladen foragers and were readily collected. For instance, the median of the „waiting time“ of a dropped paper fragment before it was collected by another worker was 2min on the 28m trail. This time also includes the handling time of the subsequent carrier. Handling time ranged from 5 to 30s. The carrier that put down the fragment usually turned back and walked towards the patch. Putting down a fragment usually took 10 to 60 s and ants regularly touched fragments with the tip of their gasters while laying them down or taking up them. Workers did not just drop the fragment on the trail, but kept touching it with antennae and mandibles even when it was already on the ground. This behaviour was clearly distinguished from that of „throwing away a fragment“, which is observed occasionally when workers clear a trail. Ants then quickly let the fragment fall, usually at the side of the trail.

Interestingly, the transport time of fragments carried by a bucket brigade on the long trail was significantly longer than that of fragments carried by a single carrier (Median, Quartile range; single carrier: 28min, 9.5, n=14; bucket brigade: 36min, 12, n=20; U=72, Z=2.4, $p<0.05$).

Within a bucket brigade, the distances covered by the participants on the long trail were very different (Fig. 4). The first carriers usually covered only a short distance. Mean transport distance covered by first carriers was 5.0±5.4m (n=22), by middle carriers 5.3±6m (n=17), and by last carriers 16.6±8m (n=22). Thus, fragments were mainly transported by the last carriers.

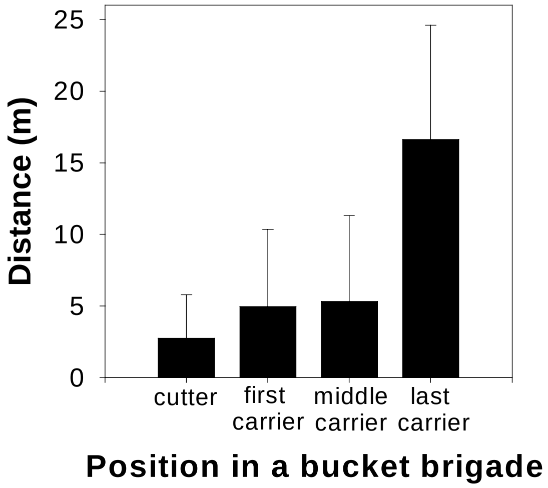


Fig. 4:
Transport distance of cutters, first, middle and last carriers in a bucket brigade on the 28m-long trail. Cutters, first and middle carriers only covered short distances.

In order to analyse whether ant body mass or load size influenced both the probability of formation of bucket brigades and the position of a given individual within it, body size of the different carriers in a bucket brigade was compared with that of single carriers. Within bucket brigades, body mass did not differ among first, middle or last carrier, and these groups were also not different from single carriers (Kruskal-Wallis-Test: $H_{(3,75)}=0.44$, p=0.9). In addition, neither fragment mass nor fragment length differed significantly between bucket brigades and single carriers (fragment mass: U=130, n=16/22, p=0.2, NS; fragment length: U=119.5, p=0.09, NS).

Regarding size-matching between body and load, body mass of last carriers in a bucket brigade, i.e., those that covered the longest distance (see Fig. 6), significantly correlated with load mass but not with load length (load mass: y=1.1+0.9x, $r^2=0.39$, $p<0.05$; load length: y=14.6+1x, $r^2=0.15$, p=0.2, NS). In contrast, body size of the first carriers neither correlated with load mass nor with load length (load mass: y=10.7-0.2x, $r^2=0.02$, p=0.9, NS; load length: y=21.5+0.2x, $r^2=0.008$, p=0.6, NS). Ant body mass of single carriers correlated neither with load length nor with load mass (Spearman Rank Correlation Test: load mass: y=6.7-0.006x, $r^2=0.00003$, p=0.2, NS; load length: y=22.4-0.4x, $r^2=0.02$, n=16, p=0.4, NS).

Bucket brigades at a natural food source

As observed in the experiments with paper plants, most cutters harvesting fragments out of *Cyperus* at 10m from the nest dropped them after cutting (42%) or laid them down after less than one meter of transport (27%), i.e., shortly after reaching the main trail. When considering the fragments that arrived at the nest, the cutters carried only 17% of them. A single carrier carried 47% of the fragments, and 36% of the fragments were transported with a bucket brigade (Fig. 5). When natural and paper fragments are compared, plant fragments were transported slightly more often with a bucket brigade than paper fragments (Chi-Square-Test: $\chi^2=4.00$, $p=0.05$), indicating that paper fragments were not dropped as an experimental artefact. This is also indicated by the comparison of the "waiting times": The median values on the 10m trail were 2min 9s (n=29) for the natural fragments, and 2min 30s for the paper fragments, values were not statistically different (U=492, Z=-0.4, p=0.7, NS).

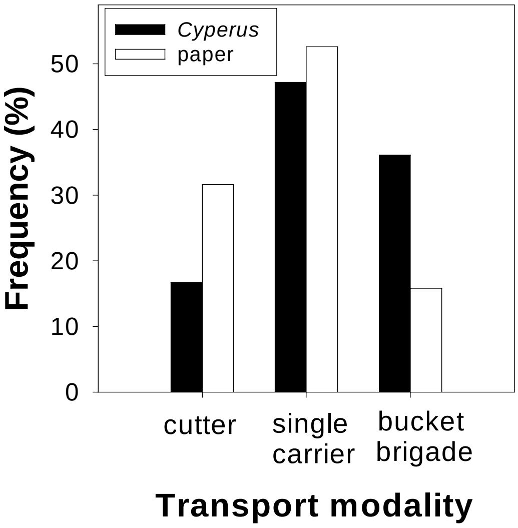


Fig. 5:
Modality of load transport for natural fragments of *Cyperus entrerrianus* and for fragments cut out of "paper plants", at 10m from the nest. Bucket brigades occurred slightly more often when workers carried natural fragments (p=0.05).

Discussion

Workers of the grass-cutting ant *Atta vollenweideri* use multi-stage foraging strategies with elaborated task partitioning. In a first stage, cutting and carrying of fragments were clearly separated activities fulfilled by distinct worker groups differing in body size. Roces and Lighton (1995) and Wetterer (1991a) showed that leaf-cutting is an energetically extremely intense activity, with workers showing metabolic rates 30 times higher than during resting. Carrying a load is less energy demanding: metabolic rates increase by a factor of 7 in unladen workers, and by 11 in loaded workers (Lighton *et al.* 1987; Roces and Lighton 1995). Thus, the energetic cost for carrying a load is approximately 3 times lower than that of cutting, but load carriage might demand a considerable time investment. Foraging trails of both leaf- and grass-cutting ants often exceed

100 metres in length, i.e., single ants may need several hours for a single foraging trip (Lewis *et al*. 1974; Weber 1972). As a result, *Atta vollenweideri* colonies seem to allocate large workers to the energy-demanding activity and small ones to the time-consuming activity.

Division of labour between cutters and carriers was observed for workers harvesting different grass species (*Paspallum* and *Cyperus*), as well as the artificial “paper plants”. And it also occurred on trails of different length. Interestingly, the frequency of fragment dropping immediately after cutting did not differ between trails of different length, suggesting that the behaviour of cutters once at the cutting place was independent of the distance from the nest. Yet, the percentage of cutters carrying their fragment directly to the nest differed between short and long trails. This might not result from behavioural differences, but rather from the fact that the distances covered by the cutters were variable. As they did not place their fragments on piles at a particular location on the trail, and considering that the covered distance neither correlate with the ant nor with the load size, it seems conceivable that workers differed in their threshold to drop the carried fragments. As a consequence, some “high-threshold” workers on short trails may arrive at the nest before their threshold for dropping is reached, whereas on long trails they might drop the fragments directly on the ground.

However, when the harvested plant was very close to the nest and no physical trail was present, the behaviour of cutters changed, so that significantly less fragments were dropped than at a distance of five meters. Thus, no division of labour occurred at such close food sources, and cutters often transported their fragments directly to the nest.

A striking task partitioning occurred during transport of fragments. On the long trail, more than half of the fragments were transported by bucket brigades, i.e., beside the cutter mostly two or three carriers transported the load consecutively. The first carrier in a bucket brigade generally dropped the load within the first meters. This occurred with similar frequency in both the artificial paper plants and the *Cyperus* plant, thus an experimental artefact could be excluded. What are the reasons for the occurrence of bucket brigades, and what variables motivate workers to drop their fragments? First, ants might decide to drop fragments that are not sufficiently attractive, thus rejecting them. But as nearly all dropped fragments were retrieved again, and the time a fragment was “waiting” for transport was short, this appears very unlikely. In addition, the “careful” lying down of the fragment, opposite to the rare “throwing away” described above, does not support these arguments.

Dropping of a load might have occurred because of the ratio between ant and fragment size, i.e., either the carrier was too small for the fragment, or the fragment too large to be carried. This seems plausible when the detrimental effects of large loads on transport rates are taken into account (Röschard and Roces 2002c; Chapter 3). Yet, the first carriers in a bucket brigade were not smaller than single carriers, nor were their loads heavier or longer than those transported by single carriers. Fragments varied considerably in length, mass and width with a considerable variance, thus I cannot totally exclude that possible load-carriage effects might have been masked by the variance. Nevertheless, this argument seems rather weak. Interestingly, fragment size correlated with worker size only for the last carriers, i.e., those that covered the longest distance, but not for the first carriers. Thus, sequential transport leads to a better size-matching between worker and load, a phenomenon similar to that recently reported for the seed-harvesting ant *Messor barbarus* (Reyes-López and Fernández-Haeger 2001). Whether loads were dropped because they did not match the ant's size or whether there was no size matching because loads anyway were only carried for a short distance, remains unresolved at this stage. However, as body mass of single carriers also did not correlate with load size, the former seems unlikely.

A tempting hypothesis concerning the adaptive value of bucket brigades refers to the efficiency of leaf transport. Sequential transport via a bucket brigade might be faster than transport by single carriers, thus enhancing material intake rates. For the sake of simplicity, I would like to term these arguments the "economic-transport-hypothesis". It should be noted that "economic" refers in this context to the maximisation of the leaf's transportation speed, which at the colony level may result in an increase in the overall rate of resource transportation. Maximisation of leaf transportation has been proposed for workers of three leaf-cutting ants species that transfer loads or cache fragments on the ground (Anderson and Jadin 2001; Fowler and Robinson 1979; Hubbell *et al*. 1980). Direct leaf transfer between *Atta colombica* workers, which occurs only in 9% of the transported fragments, resulted in higher transportation speed, although transferred fragments did not travel faster that those not transferred (Anderson and Jadin 2001). In the granivorous ant *Messor barbarus* and the social wasp *Polybia occidentialis,* transport times in bucket brigades were shorter than those observed in single carriers (Jeanne 1986b; Reyes-López and Fernández Haeger 1999). In our study, however, transport time of fragments carried by a bucket brigade was 25% *longer*, in average 8 minutes, than that of fragments carried by a single worker all the way to the nest. This was probably due to both the waiting time of fragments, and the handling time of the subsequent foragers. Differences in travel speed between carriers in a bucket brigade and single carriers are unlikely, as there were no differences in body size. Thus, in terms of foraging time, sequential transport via a bucket brigade was less efficient than transport with single carriers.

So why grass-cutting ants build up bucket brigades, when no transport costs appear to be saved and transport time increases instead of decreasing? I suggest the following scenario: The sequential transport of fragments leads to an increase in the information flow along the foraging trail, which may result in an increase in the overall rate of resource transportation. Based on this "information-transfer hypothesis", the behavioral response of dropping or passing fragments may have been selected for because of its positive effect on the information flow, rather than for an improvement in the economics of load-carriage.

Whether bucket brigades indeed accelerate the transfer of information regarding the plants actually being harvested remains at present elusive, but it is important to emphasize some processes that may contribute to a quick transfer of information, and therefore to a rapid build-up of workers at the discovered source. First, fragment dropping may allow workers to quickly go back to the food source, making it easier for them to find again the source following the freshly-deposited pheromone trail (Hubbell *et al*. 1980). More important, moving along a short trail sector during foraging may enable workers to reinforce the pheromonal marking of that trail sector much stronger than if they walk all the way to the nest. Hence, recruitment might be reinforced, leading to a quicker monopolisation of the food source, as demonstrated for first carriers of the leaf-cutting ant *Atta sexdens* (Hubbell *et al*. 1980). In this line of arguments, I usually observed first carriers turning back and returning to the patch after dropping their loads (unpublished results, see also López et al. 2000). Second, the fragments dropped on the trail, or being carried along it, may themselves act as information signals. It has been shown that leaf-cutting ant foragers are conditioned to the odours of the resources being harvested, and that worker responses at the patch depend on what nestmates are currently carrying on the trail (Howard *et al*. 1996; Roces 1990b; Roces 1994). A fragment on the trail might have a similar effect as stimulus for olfactory conditioning to occur. Fragments dropped on the ground were very attractive for unladen workers. Most workers antennated them upon finding, but continued their way to the patch without retrieval. Thus, beside the information foragers may obtain directly by contacting laden nestmates along the trail, the fragment dropped on the trail may provide additional information. If so, a dropped fragment may attract and therefore “inform” more workers during its waiting time than one that is transported all the way through to the nest by a single carrier. In this hypothetical scenario, information flow may be favoured at the expense of a reduced material intake rate at the individual level. This may result in higher colony intake rates, because other workers may be informed and participate the collective foraging. Interestingly, bucket brigades occurred slightly more often for *Cyperus* plant fragments than for paper fragments, suggesting that the occurrence of sequential transport may depend on resource quality, as the information-transfer hypothesis predicts (Roces and Núñez 1993).

The existence of a trade-off between individual harvesting rate and information flow has been reported for the leaf-cutting ant *Acromyrmex lundi* (Roces and Núñez 1993). Scout workers were exposed to droplets of scented sugar solution of either 1% or 10% concentration. Scouts detected these droplets and returned to the colony, leaving a chemical recruiting trail. When the recruits arrived, they encountered, not sugar solution, but sheets of Parafilm impregnated with the same scent, containing no sugar. Thus, no matter to which solution ants were recruited, they found the same source and cut fragments. Workers recruited to the originally 10% solution cut smaller fragments, ran back to the colony faster and showed pheromone-depositing more often than 1%-

recruits, in spite of cutting the same material. Because of the smaller size of the fragments, 10%-recuits run faster than 1%-recruits. Greater velocity did not compensate for the reduction in fragment size: 10%-recruits, despite their higher velocity, showed a *lower* rate of leaf transport to the nest than 1%- recruits. Why did they cut smaller fragments? The authors argued that by cutting and carrying smaller fragments, ants decrease time per roundtrip and so “sacrifice” individual delivery rate in order to return earlier to the colony for further recruitment (see also Roces 1993). In a very similar way, first carriers in our study may “sacrifice” their individual delivery rate so as to return earlier to the source in order to continue collecting and recruiting.

Information transfer for quick recruitment of nestmates appears particularly relevant when the dynamics of the foraging patterns of *A. vollenweideri* is considered. At the end of the foraging trails, workers spread out and harvest a given patch containing several grass plants. Workers rarely deplete the complete patch, but kept switching to new, neighbouring patches every few days (unpublished observations). The reasons for these responses remain unclear. A rapid induction of secondary, deterring compounds in the harvested plant, which makes the plants unpalatable, or differences in plant quality may play a role (see Vicari and Bazely 1993), but there are no studies on this phenomenon. Whatever the reasons, such frequent switching needs a communication system enabling ants to respond quickly.

Up to now, both the information-transfer-hypothesis and the economic-transport-hypothesis remain at the descriptive level, as no predictions of them have been experimentally addressed. For instance, if bucket brigades are formed in order to speed up leaf transport, bucket brigades should be expected to occur when the transporting ants move too slow, for example when ants carry, relative to their size, very large fragments. Based on the information-transfer-hypothesis, bucket brigades are expected to occur more frequently under conditions in which information is worth transferring, for instance when workers harvest high-quality resources or the colony is starved (Roces and Hölldobler 1994). Field experiments aimed to explicitly test the predictions of both hypotheses are already under way.

Sequential transport via bucket brigades in the grass-cutting ant *Atta vollenweideri*: Load-carriage effect or information transfer?

Summary. Foraging workers of the grass-cutting ant *Atta vollenweideri* form bucket brigades consisting of a cutting worker and several carriers that transport the load consecutively. In this study I tested the predictions of two hypotheses concerning the causes for the occurrence of bucket brigades: First, the “economic-transport-hypothesis” predicts that workers may transfer fragments, thus leading to the formation of bucket brigades, because loads are either too large for the carrying ant, or the ants are too small for the loads they carry, thus rendering transport inefficient. As a consequence, the probability of occurrence of bucket brigades is expected to depend on fragment size independent on fragment quality, being higher for larger fragments that are difficult to carry. The “information-transfer-hypothesis”, conversely, suggests that the behavioral response of transferring fragments may have been selected for because of its positive effect on the information flow, rather than for an improvement in the economics of load-carriage: By dropping the load a worker may return earlier back to the foraging site and be able to reinforce the chemical trail, thus enhancing recruitment. In addition, the transferred fragments may themselves act as information signals about what plant is currently harvested, thus enabling workers to choose among sources of different quality or search specifically for them. This hypothesis predicts that the formation of bucket brigades should strongly depend on fragment quality, and be independent of fragment size for a given quality. To distinguish between these alternatives, workers from a field colony were presented with standardised paper fragments that differed either in size or in quality. The occurrence of bucket brigades was quantified by following marked grass fragments all their way to the nest and by recording the number of transfers between carriers, the distances covered by each one, and their body size. Additionally, the transport time of fragments carried by a bucket brigade was compared to that of fragments transported by single carriers all the way to the nest. Results indicate that neither an increase in fragment mass nor in fragment length modifies the frequency of occurrence of bucket brigades. In addition, transport via bucket brigades took longer than if it was accomplished by a single carrier all the way through. However, the frequency of occurrence of bucket brigades increased with increasing fragment quality independent of its size. In addition, high-quality fragments were transferred after shorter distances, i.e., more attractive loads were dropped more frequently and after a shorter distance than less attractive ones, with the first carriers returning to the foraging site to continue foraging. Taken together, results suggest that rather than enhancing the economic of load carriage at the individual level, the occurrence of bucket brigades increases the information flow at the colony level.

Introduction

During the last two decades an increasing number of studies uncovered sequential processing of material in a variety of social systems such as ants (Fowler and Robinson 1979;

Hubbell *et al*. 1980; López *et al*. 2000; Pfeiffer and Linsenmair 1998; Reyes-López and Fernández Haeger 1999), bees (Hart and Ratnieks 2000b; Seeley 1989b), wasps (Jeanne 1986b), and humans (Bartholdi *et al*. 2001). In general, these bucket brigades occur in the context of foraging, but they were also shown for nest building (Jeanne 1986b) and waste management (Hart and Ratnieks 2001).

The main benefits of a sequential compared to a non-sequential material processing often result from both an increased material turnover (Bartholdi *et al*. 2001), and a decrease in the time (and energy) required to perform the activity (Reyes-López and Fernández Haeger 1999), so as to accelerate, for instance, the depletion of ephemeral food sources (López *et al*. 2000).

Similar advantages were proposed for the bucket brigades formed by foraging leaf-cutting ants. For instance, in *Atta sexdens* and *A. cephalotes*, arboreal foragers cut leaves at their stems and dropped them. On the ground, foragers from a second group, the “cache exploiters”, cut transportable pieces out of these dropped leaves and carry them to the main trail. There, loads are dropped and retrieved by a third worker group that carries them to the nest (Fowler and Robinson 1979; Hubbell *et al*. 1980). The specialisation between cutters and carriers benefits the colony by saving the time and energy of dozens of trips up and down the trees. Task partitioning between the carriers may in addition have the advantage that the cache exploiters might easier find their way back to the source when they are specialised in their role. Task partitioning was also recently reported in *Atta colombica* during load transport, with fragments being directly transferred or cached on the trail in 21% of the cases (Anderson and Jadin 2001). Direct leaf transfer between workers, which occurred in only 9% of the transported fragments, resulted in higher transportation speed, although transferred fragments did not travel faster than those not transferred. The authors conclude that fragments might be dropped or transferred if a minimum transport speed is not met by the carrier (Anderson and Jadin 2001). Although it seems conceivable that loads carried particularly slow may eventually be abandoned by the carrier, a low travel speed does not necessarily indicate that a worker is not capable of carrying the load or of walking faster. Travel speed may be reduced as a consequence of trail-marking activity by the carriers walking from the food source to the main trail. Or workers may slow down not because of the load size, but also for the reason that they try to pass the fragment to an unladen nestmate in order to return to the source.

The question arises whether the adaptive value of bucket brigades in leaf-cutting ants refers to the efficiency of leaf transport. Sequential transport via a bucket brigade would be expected to be faster than transport by single carriers, thus enhancing material intake rates. This “economic-transport-hypothesis” (Röschard and Roces 2002c; Chapter 4) predicts that fragments might be dropped because loads are either too large for the carrying ant, or the ants are too small for the loads they carry, thus rendering transport inefficient. It should be noted that “economic transport” in this context refers to the maximisation of the leaf’s transportation speed, which at the colony level may result in an increase in the overall rate of resource transportation. As a consequence, sequential transport via bucket brigades might allow a quicker transport of loads, thus saving foraging time, as shown for the seed-harvester ant *Messor barbarus* (Reyes-López and Fernández Haeger 1999). However, recent investigations on the grass-cutting ant *Atta vollenweideri* showed that transport times of fragments carried by bucket brigades were *longer* than that of fragments carried by a single worker all the way to the nest (Röschard and Roces 2002c; Chapter 4), leaving the issue unresolved.

Alternatively, sequential transport of fragments via bucket brigades might lead to an increase in the information flow along the foraging trail, which may result in an increase in the overall rate of resource transportation. Based on this "information-transfer hypothesis" (Röschard and Roces 2002c; Chapter 4), the behavioral response of dropping or passing fragments may have been selected for because of its positive effect on the information flow, rather than for an improvement in the economics of load-carriage. The importance of information transfer is apparent when the colony-wide foraging patterns of leaf-cutting ants are considered. Foraging trails can exceed 100 m in length (Lewis *et al*. 1974; Weber 1972) and are characterised by strong branching into several side trails. Thus, outgoing workers have to choose between several crossings leading to different food patches. Bucket brigades could enhance information transfer in several aspects. By dropping a load at the trail crossing, successful workers may be able to return to the foraging site earlier following a freshly-deposited pheromone trail. More important, moving along a short trail sector during foraging may enable workers to reinforce the pheromonal marking of that trail sector much stronger than if they walk all the way to the nest. Hence, recruitment might be reinforced, leading to a quicker monopolisation of the food source, as demonstrated for first carriers of the leaf-cutting ant *Atta sexdens* (Hubbell *et al*. 1980). Furthermore, fragments dropped on the trail, or being carried along it, may themselves act as information signals about what plant is currently harvested, thus enabling workers, via olfactory conditioning (Howard *et al*. 1996; Roces 1990) to choose among sources of different quality or search specifically for them. The "information-transfer-hypothesis" predicts that foragers carrying highly-attractive fragments should therefore be more motivated to inform than foragers carrying less-attractive loads, i.e., to transfer or drop their fragments so as to promote the formation of bucket brigades.

In order to investigate the benefits of bucket brigades in leaf-cutting ants, foraging behaviour of the grass-cutting ant *Atta vollenweideri* was investigated in the field. Grass-cutting ants provide a particularly well suited system for studies of bucket brigades and foraging behaviour because ants forage on monocotyledonous plants near the ground (Jonkman 1976), so that the whole process of harvesting from the source on until reaching the nest can be observed and experimentally manipulated. A recent study on *A. vollenweideri* revealed that foraging was partitioned in several stages: Cutters drop their grass fragments or carry them to the ground, and a second group retrieve the pieces and carry them to the main trail or a short distance along it. The loads are finally retrieved by a third group of foragers and transported to the nest (Röschard and Roces 2002c; Chapter 4). The aim of the present study was to test predictions derived from both the "economic-transport-hypothesis" and the "information-transfer-hypothesis" (Röschard and Roces 2002c; Chapter 4). The economic-transport-hypothesis predicts that the probability of dropping a fragment, i.e., the probability of occurrence of bucket brigades, should depend on fragment size independent on fragment quality, being higher for larger fragments that are difficult to carry. The information-transfer-hypothesis, conversely, predicts that the formation of bucket brigades should strongly depend on fragment quality, and be independent of fragment size for a given quality. To distinguish between these alternatives, workers from a field colony were presented with standardised paper fragments that differed either in size or in quality. The occurrence of bucket brigades was quantified by following marked grass fragments all their way to the nest and by recording the number of transfers between carriers, the distances covered by each one, and their body size. Additionally, the transport time of fragments carried by a bucket brigade was compared to that of fragments transported by single carriers all the way to the nest.

Material and Methods

Field experiments were conducted in September 2000 at the biological field station of the "Reserva Ecológica El Bagual" in Formosa province, Chaco region of north Argentina, on a mature colony of *Atta vollenweideri*. Ant foraging activity was nocturnal, so that headlamps covered with a red filter were used for observations. Foragers showed no signs of disturbance because of the light.

The effects of load size on the occurrence of bucket brigades were investigated on a natural trail of approximately 50 m length on which ants harvested a variety of grass species. At a distance of 33 m from the nest, ants were presented with three types of fragments which were placed in the middle of the trail. Fragments differed either in length or in mass, but not in width, which was held constant at 3mm. "Short" fragments were 15 mm long and weighed in average 4.25 mg. "Long" fragments were 30 mm long with an average mass of 8.5 mg. Finally, "double" fragments were made by sticking two wet fragments together, forming a short double fragment of 15 mm in length, and an average mass of 8.5 mg. These fragment types were chosen in order to separate the effects of load length and load mass on transport speed. It has been recently shown that for fragments of similar mass, a two-fold increase in fragment length had a marked negative effect on manoeuvrability during transport and, as a consequence, on material transport rate (Röschard and Roces 2002c; Chapter 3). Fragments were cut out of standard paper ($80 g/m^2$), soaked with orange juice for at least one hour, and then dried. In order to increase the attractivity of the paper fragments presented on the trail, I additionally placed an artificial "paper plant" 20 cm farther, beside the main trail. It was created by soaking paper stripes of 15 cm length in orange juice, and by putting the stripes into a small plastic vial that was "planted" on the ground, as recently described (Röschard and Roces 2002c; Chapter 4). Ants readily harvested the paper plant and dropped fragments on the trail as observed for natural grass plants (Röschard and Roces 2002c; Chapter 1). During the measurements, however, only the experimental, previously cut fragments were monitored. Such fragments were identified with pencilled marks and placed on the trail. After retrieval by workers, fragments were followed all their way to the nest. The occurrence of sequential transport, transport time, transport distance by each involved worker, as well as the "waiting times" of fragments, i.e., the time a fragment was left on the trail before being retrieved by another worker, were recorded for each individual fragment. For those fragments transported by a bucket brigade, total transport time included travel time, handling time by the foragers and waiting times of the fragment.

In order to investigate the effect of food quality on the occurrence of bucket brigades, ants were presented with paper fragments of constant size that were previously treated either with pure orange juice (henceforth: "orange fragments"), with a solution of 15% tannin in orange juice (henceforth: "tannin-orange fragments"), or with a solution of 10% tannin in water (henceforth: "tannin-water fragments"). Tannin is a natural plant secondary compound that has been shown to negatively influence leaf-cutting ant foraging and to inhibit the ant symbiotic fungus (Cherrett *et al*. 1989; Littledyke and Cherrett 1976). Fragments impregnated with these solutions are therefore expected to differ in quality, and vary in their attractivity to the ants. Differences in attractivity were measured prior to the experiments by presenting simultaneously one fragment of each quality on the trail in 20 m distance from the nest and recording which one was taken first (see results). A trail that bifurcated into two branches at 31 m distance from the nest was used for the quality-experiments. On both sides at 33 metres distance from the nest, ants were presented with fragments of two different qualities. During four consecutive nights, orange fragments were compared with tannin-orange fragments. The side of presentation was alternated each night in order to control for potential side effects. In the following two nights, ants were presented in the same manner with orange fragments and tannin-water fragments, but due to methodological difficulties only tannin-water fragments could be followed. All fragments were 20 mm long, 3 mm wide and averaged 9 mg. Again, "paper plants" of the respective quality were presented 20 cm farther beside the trail, but only the experimental fragments were followed. A total of 42 orange and tannin-orange fragments and 35 tannin-water fragments was followed.

Results

Behaviour of the first carriers

The occurrence of bucket brigades strictly depends on the behaviour of the first worker that retrieves a fragment. They were formed when this “first carrier” transferred its fragment to a nestmate or dropped it after a given distance, and a nestmate further retrieved the fragment. A total of 16 marked first carriers were therefore followed after collection of orange fragments placed at 33 m from the nest, and their behaviour monitored. As mentioned in the method section, a “paper plant” was placed 20 cm further. Observations lasted at least 45 to 60 min, or until the carrier entered the nest.

All first carriers were observed to continue foraging at the location where they had collected the initial paper fragments, and retrieved at least one further fragment. Only one worker switched to another foraging site and continued foraging, but collected small natural sticks. Seven carriers returned to the nest during the observation time. Most carriers additionally collected one or two further fragments prior to entering the nest, and were possibly at the end of their foraging period. Seven ants collected more than five further fragments and started to walk back once more to the patch during the observation time. Thus they were still within their foraging period when they were caught (Fig. 1). The first carriers did not cut any fragment, with the exception of two ants that cut one fragment each out of the paper plant after having collected several paper fragments. All other ants did not cut, even though some of them approached the paper plant. Carriers did not show a preferred location to drop their fragments, i.e., they did not walk a constant distance before dropping it. Even the distances covered by individuals that retrieved several fragments varied considerably.

General description of bucket brigades

Most bucket brigades consisted of two or three carriers, but I occasionally observed up to five foragers. When not directly transferred, fragments were dropped in the middle of the trail. Ants neither preferred certain places on the trail for dropping fragments, nor did they build up piles at a given location. Dropped fragments attracted unladen foragers and were readily collected. Ants regularly touched fragments with the tip of their gaster while taking up or lying down a fragment. Waiting time of fragments that were initially deposited by us, i.e., fragments that were not previously touched by the ants, was significantly longer than the waiting time of those dropped by the first carriers, suggesting that fragments were chemically marked by ants when touching them with their gaster or mandibles (untouched fragments, all fragment sizes pooled: mean ± SD: 139 ± 166 sec, n=141; fragments deposited by first carrier: 44 ± 88 sec, n=114; U-test: U= 2412, Z= 7.2, $p<0.0001$).

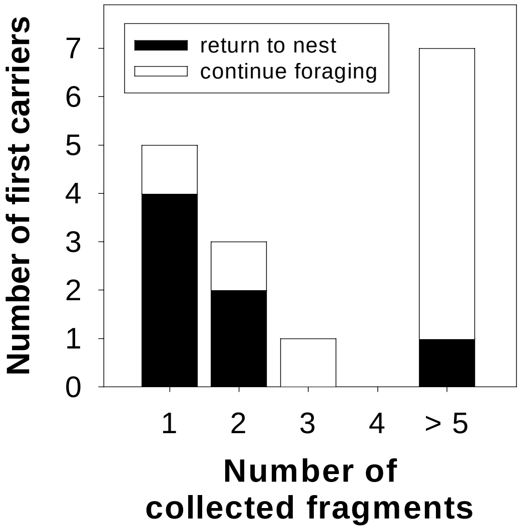


Fig. 1:
Number of additional fragments collected by the first carriers in a bucket brigade after the first fragment was dropped or transferred. Black indicates foragers that returned to the nest with a fragment during the observation time. White indicates foragers that turned back to the patch at the end of the observation time.

With regard to the mode of fragment transfer, 29% (range 14-54%) of all transfers between first and second carrier were direct and no dropping occurred. The proportion of direct transfers to the total number of transfers was independent of both fragment size and food quality (Chi-Square-Test: $p>0.05$ for all pairs).

Based on direct observations, it was difficult to reveal what variables triggered a direct transfer between workers. In some cases, the first carrier was observed to reduce its walking speed and move very slowly until a nestmate approached and took the fragment. In other cases, the carrier kept approaching unladen nestmates coming from the nest, whereby it rather meandered along the trail instead of walking straight ahead towards the nest. Additionally, unladen nestmates were observed to approach the first carrier, to antennate the fragment and then to take it. Several times both ants were observed to struggle for one or two minutes until one of them gave up and the other took the fragment.

Load-carriage effects

Frequency of occurrence of bucket brigades was independent of the size of the fragments transported (Fig. 2). Fifty-seven percent of the long fragments (n=46), 69% of the double (n=52), and 55% of the short fragments (n=47) were carried by bucket brigades. These differences were not statistically significant (Chi-Square-Test: each pair p>0.2). Similarly, the distance each fragment was carried by the first carrier was independent of fragment size (Fig. 3; mean ± SD; *long*: 11.9 ± 9.9 m, *double*: 7.0 ± 6.0 m, *short*: 8.2 ± 7.2 m; Kruskal-Wallis-Test: $H_{(2,88)}$=2.9, p=0.2, NS).

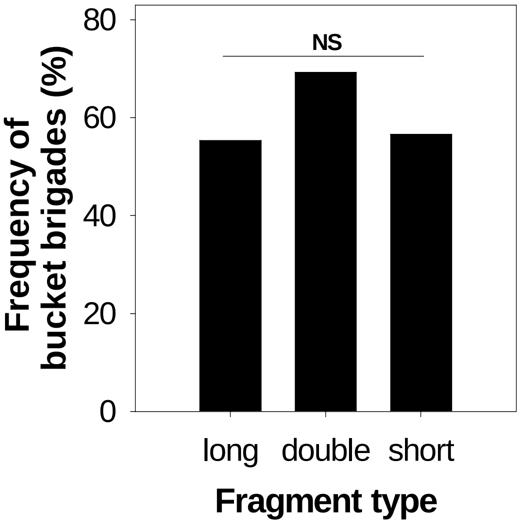


Fig. 2:
Frequency of occurrence of bucket brigades for ants collecting fragments of different sizes but constant quality.

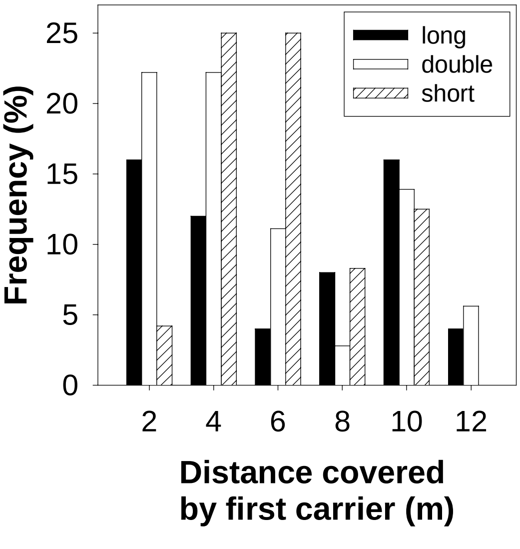


Fig. 3:
Distance at which first carriers in a bucket brigade transferred their fragments. Bars indicate how many loads of a specific size were transferred within a distance category (bin width: 2 m). Fragments were presented at “0 meters”, and 100% refers to all transferred fragments. Trail length was 33 m. Transport distance of loads of different size did not differ significantly.

As *Atta* worker are highly polymorph, I compared body size distribution of the different task groups (single, first and last carrier within bucket brigades), in order to investigate possible relationships of ant body size with either the occurrence of or the position in a bucket brigade. For all fragment types presented, first carriers in a bucket brigade were smaller than last carriers. First carriers were also smaller than single carriers, i.e., those that transported the fragments all the way to the nest, for long and short fragments, but not for double ones. Body size of single and last carrier did not differ statistically (see Appendix below). Furthermore, first carriers of long fragments were larger than first carriers of short fragments ($H_{(1,52)}=10.9$, $p<0.005$). The same was true for last ($H_{(1,50)}=9.7$, $p<0.005$) and single carriers ($H_{(1,39)}=6.4$, $p<0.05$). Thus, the size of the carriers in a bucket brigade depended on both their position within it and the load size carried.

In order to investigate whether the dropping distance was dependent of ant body size, distances covered by the first carriers were analysed as a function of body mass. For long and short fragments, a relationship, though not significant, between body mass of first carriers and covered distance was found, but the sign of the correlation differed between groups, and correlation coefficients were small. No correlation was found for the double fragments (Spearman Rank Correlation Test: long: $y=x-0.6$, $r^2=0.16$, $R=0.39$, $t=2.09$, $n=26$, $p=0.05$, NS; double: $y=-0.2x+9.9$, $r^2=0.06$, $R=-0.24$, $t=-1.41$, $n=34$, $p=0.2$, NS; short: $y=-0.3x+10.5$, $r^2=0.03$, $R=-0.41$, $t=-2.02$, $n=24$, $p=0.06$, NS). Hence, the distance a load was carried before dropping was independent of ant body mass.

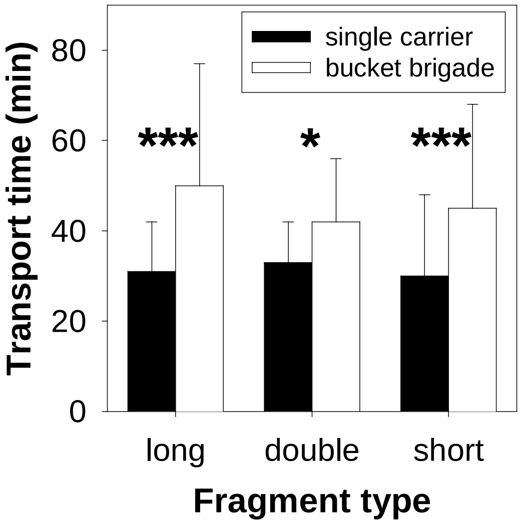


Fig. 4:
Transport time (mean ± SD) of fragments transported by one carrier all the way to the nest (black bars) or by a bucket brigade (white bars). Transport time includes handling time of foragers and waiting times of dropped fragment until transport was continued. Transport by a bucket brigade took significantly longer (* p<0.05, *** p<0.001).

The transport time of fragments carried by a bucket brigade over 33 m was significantly longer than that of fragments carried by a single carrier all the way through, with differences ranging form 9 to 18 min (Fig. 4, mean ± SD, long fragments: 31 ± 11 min (single carrier), 49 ± 27 min (bucket brigade), U-test: U=86.5, Z=4.0, p<0.0001; double fragments: 32 ± 9 min (single carrier), 41 ± 14 min (bucket brigade), U=174.5, Z=2.3, p<0.05; short fragments: 30 ± 18 min (single carrier), 44 ± 23 min (bucket brigade), U=103, Z=3.5, p<0.001).

<u>Effect of fragment quality</u>

The three fragment qualities presented were indeed ranked by the ants in the choice experiment. Workers took first the orange fragments in 56% of the cases, the tannin-orange fragments in 28%, and the tannin-water fragments in 16% of the cases (Chi-Square-Test, p<0.05 for all pairs, n=39). Thus, orange-fragments were clearly the most attractive ones.

Bucket brigades occurred significantly more often for the most attractive fragments (orange) than for the two others (Fig. 5): 81% of the orange fragments (n=41), 57% of the tannin-orange fragments (n=42), and 40% of the tannin-water fragments (n=35) were transported by bucket brigades (Chi-Square-Test: orange vs. tannin-orange: p<0.05; orange vs. tannin-water: p<0.0005; tannin-orange vs. tannin-water: p=0.2, NS). These values correspond to all fragments presented over the entire experimental period.

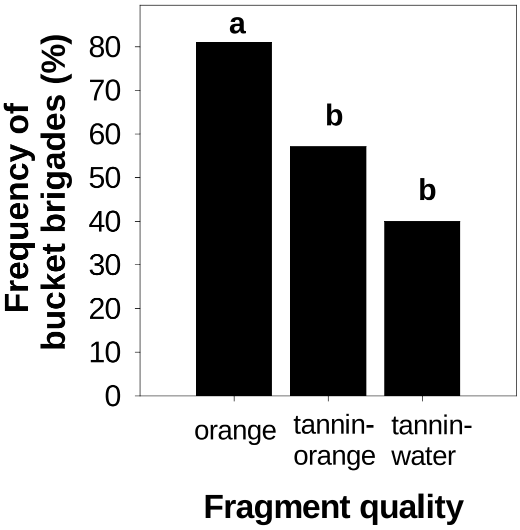


Fig. 5:
Frequency of bucket brigades for ants collecting fragments of different quality but constant size. Bars sharing the same letter are not statistically different. Bucket brigades occurred significantly more often for high-quality fragments.

Interestingly, the probability of occurrence of bucket brigades changed over the course of the experiment. When orange and orange-tannin fragments were compared, orange fragments were dropped slightly more often than tannin-orange fragments in the first experimental night (88% vs. 71%, respectively). However, this difference strongly increased over the course of the following nights (Fig. 6). The occurrence of bucket brigades for tannin-orange fragments declined over the following nights to a value of 38% (3 out of 8 fragments) at the fourth night, whereas that for orange fragments increased over the same period and reached 100% (10 fragments). The tannin-water fragments are not compared here as no data are available for the orange fragments presented simultaneously on the other side of the fork.

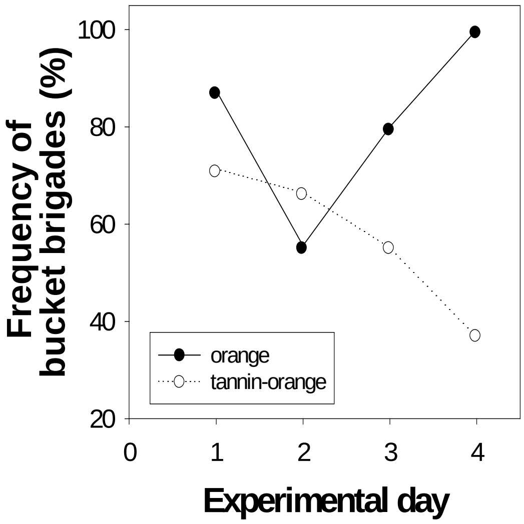


Fig. 6:
Occurrence of bucket brigades over the whole experimental period of four days. Closed symbols represent orange fragments and open symbols tannin-orange fragments. Each day at least seven fragments of each quality were followed.

Fragment quality also affected the distance the first carrier covered before dropping or directly transferring a fragment: The highly attractive orange fragments were dropped after a significantly shorter distance than the less attractive tannin-orange fragments (Fig. 7; mean ± SD; orange: 6.1±7.2 m; tannin-orange: 12.6 ± 9.9 m; $H_{(1,57)}$=7.6, p<0.01). Thus, high quality fragments were dropped more often (Fig. 5) and after shorter distances than fragments of lower quality. In addition, the place where direct fragment transfers occurred was also dependent of quality: Orange fragments were directly transferred after distances much shorter than those at which tannin-orange fragments were transferred (mean ± SD: orange: 6.9 ± 5.5 m, n=8; tannin-orange: 21.2 ± 6.2 m, n=6; $H_{(1,14)}$=7.4, p<0.01). As for the fragments of different size, the distance covered by the first carriers was independent of their body mass (Spearman Rank Correlation Test: orange: R=-0.16, n=32, p=0.4, NS; tannin-orange: R=-0.38, n=23, p=0.07, NS; tannin-water: R=-0.13, n=13, p=0.7, NS).

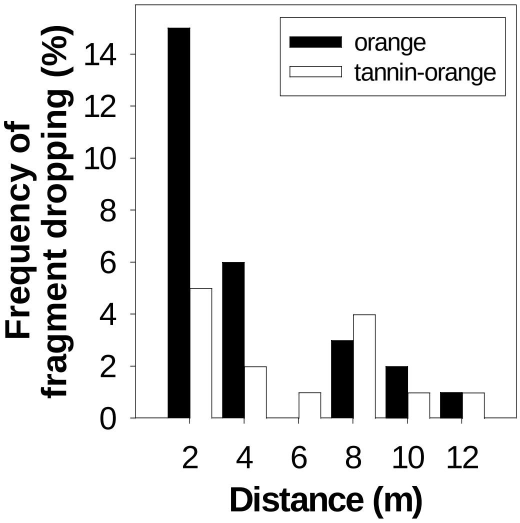


Fig. 7:
Distance at which first carriers in a bucket brigade dropped their fragments. Bars indicate how many loads of a specific quality were dropped at the specified distance, i.e. 100% refers to all transferred fragments, directly and indirectly. Some fragments were dropped after more than 12 m and thus do not appear in this figure. Fragments were presented at "0 meters". Trail length was 33 m. High-quality fragments were transferred after significantly a shorter distance than low-quality fragments.

Discussion

The present study addressed the question about the causes for the occurrence of bucket brigades during foraging in the grass-cutting ant *Atta vollenweideri*. In social insects as well as in human societies, transport via bucket brigades may result in a reduction of working time, thus leading to an increased turnover of material (Bartholdi *et al*. 2001; Jeanne 1986b; Reyes-López and Fernández Haeger 1999). Because this probably is the most intuitively expected benefit of bucket brigades, it was proposed for a number of further sequential transport systems in ants (Anderson and Jadin 2001; Fowler and Robinson 1979; Hubbell *et al*. 1980; López *et al*. 2000). Yet, in the grass-cutting ant *A. vollenweideri*, transport via bucket brigades took *longer* than if it was accomplished by a single carrier all the way through (this study and also (Röschard and Roces 2002c; Chapter 4). This was mainly due to delays associated with the "careful" lying down of the fragment, the waiting time until another worker retrieved the fragment, and the handling time of the subsequent worker. Thus, regarding the individual fragment, sequential load transport was more time consuming and therefore resulted in a lower material transport rate than the non-sequential mode.

Because ants cut and carry loads of variable size, it is plausible that fragments might be dropped because loads are either too large for the carrying ant, or the ants are too small for the loads they carry, so that transport speed is too slow (Anderson and Jadin 2001). The present results, however, contradict this prediction of the "economic-transport-hypothesis", as neither an increase in fragment mass or in fragment length, even though they markedly affect transport rates (Röschard and Roces 2002c; Chapter 3), affected the probability of occurrence of bucket brigades. In addition, larger loads would be expected to be dropped after a shorter distance than lighter ones, yet this was not the case. Finally, if fragments were transferred because of a mismatch between body and fragment size, fragments of a given size carried by small workers should be dropped at shorter distances than those carried by larger workers, yet there was no significant relationship between these variables. Therefore, no available data seem to support the predictions of the economic-transport hypothesis for the occurrence of bucket brigades.

Interestingly, first carriers were smaller than last carriers in a bucket brigade, as reported for seed-harvester ants (Fowler and Robinson 1979; Hubbell *et al*. 1980; López *et al*. 2000; Pfeiffer and Linsenmair 1998; Reyes-López and Fernández Haeger 1999), and also than single carriers that transported the fragment all the way to the nest. This may *a priori* hint to the economic-transport-hypothesis, i.e., fragments might be initially dropped because the first carriers were too small for the task to be efficiently performed. However, it is difficult to shed light on the causality of this relationship. Ants might drop the fragment because they are too small for the task. Or since they carry the fragments only for a short distance, it may pay for the colony to assign smaller workers to this task, allocating larger workers to the long-distance transport. For covering long distances it may be important to be large enough for having sufficient energy reserves to reach the nest or for being able to walk fast. In addition, observations on the collection of dropped fragments indicate that workers choose their loads very carefully: upon finding a dropped fragment, a worker first tests it by lifting it before it either abandon the fragment or take it up for carriage. It seems very unlikely that a very high percentage of foragers (up to 100% of the orange fragments in our experiments) erroneously collected fragments they were unable to carry because of their size, and therefore dropped them after a short distance. And more important, why small workers should drop these high-quality fragments more often than low quality ones, if their decisions are based alone on fragment size? The economic-transport-hypothesis fails to provide an explanation.

Fragment quality was observed to markedly affect both the frequency occurrence of bucket brigades and the distance covered by the first carrier before transfer. The first carrier dropped very attractive fragments more often and after a shorter distance than less attractive ones. Intuitively, one would expect a worker carrying a high-quality fragment to be more motivated to carry it all the way through to the nest. So why should the carrier drop the fragment? A crucial hint might be the subsequent behaviour of the first carriers: All of them continued foraging and all but one returned to the exact place where they collected the first fragment. An ant dropping a load on the main trail after carrying it for a short distance is expected to: I) be able to easier find the source again following their freshly-deposited pheromone trail back; and ii) travel more frequently on that particular trail or patch section than if it walked all the way loaded to the nest. Thus, trail-marking between the food source being exploited and the main trail could be enhanced to a much larger extent, leading to a quicker recruitment as well as a faster monopolisation of the discovered source, as demonstrated for foragers of the leaf-cutting ant *Atta sexdens* (Hubbell *et al*. 1980). It is important to note that field foraging trails can easily exceed 50 m in length. For the 33 m distance of our experiments, ants usually needed 30 to 60 minutes. This means that one single roundtrip would last one or two hours. In contrast, the first carriers I marked managed up to 13 roundtrips per hour by foraging just on their short trail section. Thus, dropping the load could serve to reinforce trail-marking and to increase recruiting activity.

Leaf- and grass-cutting ants forage along well-defined trunk trails leading to the harvested trees (in case of leaf-cutters) or grass patches (Fowler and Robinson 1979; Lewis *et al*. 1974; Weber 1972). One might be puzzled about the necessity of so much recruitment as trunk trails exist. But one has to consider that trunk trails of *Atta vollenweideri* split up into several side branches and that foraging patches not always are located directly beside a trail. This means that between patch and main trail, a distance without or with a poorly-defined trail has usually to be covered, thus making the finding of the source difficult. Moreover, workers of *A. vollenweideri* usually did not deplete sources, but switched to other plants within each few days (unpublished observations). The reason for this behaviour remains unclear. Rapid induction of secondary deterring components in the harvested plants may be responsible (see Vicari and Bazely 1993), but no studies have been carried out to present to investigate this phenomenon. Hence, the dynamic pattern of used foraging trails and the strong branching of the trails could promote the evolution of a system that allows quick information transfer.

Apart from the effect of information transfer by recruiting one can imagine another effect of load dropping. As soon as an ant started to lay down her load, unladen nestmates coming from the nest were attracted to it. Most of them walked on after having investigated the fragment. For *Atta colombica* it was shown that recruited foragers preferred to harvest the source their nestmates mainly were carrying on the specific trail irrespective of what they originally were recruited for (Howard *et al*. 1996), hence a conditioning of foragers took place (Roces 1990; Roces 1994). In a similar way, one could imagine that an attractive fragment found on the trail may condition unladen foragers on a specific source, especially if the previous carriers additionally scent highly attractive loads prior dropping. The shorter waiting times of fragments after having been carried by an ant, compared to a “naive” fragment deposited by us, strongly suggests that dropped loads may have been marked by carrying ants. The fact that ants have intramandibular glands is very interesting in this context, but the function of such secretion remains speculative (Schoeters and Billen 1994). Such a phenomenon may be relevant in the context of forking trails and changing harvesting places, which might force colonies to apply strategies allowing workers to frequently “update” information about currently harvested sources and their quality.

Of particular interest in this context is the temporal development of the occurrence of bucket brigades as a function of fragment quality. During the first two nights both the high-quality orange fragments and the low quality tannin-orange fragments were transported by an equal percentage of bucket brigades. During the following two nights, the occurrence of bucket brigades rose for orange and declined for the tannin-orange fragments. This means that the difference in transport modality I observed between the two qualities did not exist a priori, but was established during harvesting. This “delayed preference” for a transport modality suggests that a kind of feedback from inside the nest could be responsible for the different foraging strategies. This resembles the “delayed rejection” described by Knapp *et al*. (1990) in leaf-cutting ant workers harvesting leaf fragments: fragments of some plant species were first readily accepted by the workers, and in the following days no longer collected. This phenomenon was recently analysed by North *et al*. (1999): Small laboratory *Atta sexdens* colonies were fed with granules scented with orange and treated with a fungicide. Ants readily collected those baits at the beginning of the experiments, but rejected them from the second or third day on, even those granules that were untreated. The authors conclude that if the substrate causes toxic effects on the symbiotic fungus, the fungus will produce a chemical signal that would influence the ant foraging responses, because workers might then associate dead fungus with the flavours of the treated bait. However, the exact underlying mechanisms are not yet uncovered. Similarly, feedback from inside the nest may cause *A. vollenweideri* workers to apply different foraging strategies for items of different quality. Interestingly, the spontaneous preference for the orange fragments already existed at the very beginning of the experiments, as the preference tests showed. Thus, the absolute attractivity did not yet determine the frequency of occurrence of bucket brigades, but further signals were needed. Laden workers always showed frequent contacts with unladen nestmates, which in some cases resulted in a fragment transfer. Hence, carriers may receive a feedback about the quality of the carried fragment, for instance, based on how fast they find an ant taking over the load (in the case of direct transfers), or how intense and frequent they are contacted by unladen nestmates.

I hitherto considered conditions that may have lead to the evolution of bucket brigades, yet at the mechanistic level the question arises what triggers load dropping. Our results give no indication that load size or ant body size effects were involved. The correlation of body mass and covered distance I found in our experiments were weak, sometimes of different sign and showed in addition extremely high variation. Moreover, even individual ants delivered their loads over very different distances before dropping. AS mentioned above, low transport speed was proposed to trigger fragment transfers in *Atta colombica* (Anderson and Jadin 2001). I did not analyse transport speed but measured the total walking time of each carrying ant, including handling times, interactions with nestmates, etc. Considering that the trail structure changes very much with distance, i.e., further away from the nest the trail sections are generally narrower, less cleared of vegetation and with obstacles, average walking speed over the whole distance seems to be not meaningful. Importantly, I often observed foragers walking very slow or even stopping walking before dropping a load. These ants started at the source with a higher speed, thus they were able to walk faster, and then reduced their speed. This was often accompanied by a continuous approach to unladen nestmates and a typical zigzag walking pattern from one side of the trail to the other. Therefore, it seems that ants walked slow because they were going to drop their loads, instead of that they dropped their loads because of their slow walking. In addition, ants covering the section from patch to main trail possibly are involved in trail-marking, which also will slow them down. Further conditions that were shown to cause fragment dropping under laboratory conditions in leaf-cutting ants, such as “bottle necks” during transport (Hart and Ratnieks 2000a) were absent in our field study. There were in addition no specific deposition places that could have triggered dropping via positive feedback or the presence of pheromone marking (Hart and Ratnieks 2000a) since the short waiting times of dropped fragments prevented the formation of piles. One possible trigger could be the interest of unladen workers for the load as mentioned above, but this aspect needs further investigation.

To summarise the present study I can state that foraging by bucket brigades did not yield a time benefit compared to single carriers, and that bucket brigades were not affected by load size. With increasing food quality, however, frequency of bucket brigades increased and the distance of the first load dropping decreased. First carriers of a bucket brigade returned to the foraging site after dropping their load. I therefore suggest that rather than enhancing the economic of load carriage at the individual level, the occurrence of bucket brigades increases the information flow at the colony level.

Appendix

Table 1:

a) Body mass of both carriers in a bucket brigade and single carriers that transported fragments of different sizes (long, double or short fragments).

b) Statistical comparisons after Kruskal-Wallis-ANOVA.

a) ant body mass, mean ± SD (n)

	Long fragments	Double fragments	Short fragments
First carrier	12.7±4.2 mg (25)	11.4±6.1 mg (35)	8.7±4.5 mg (26)
Last carrier	19.3±10.7 mg (26)	15.5±7.1 mg (36)	13.7±9.3 mg (25)
Single carrier	16.7±5.1 mg (21)	14.0±7.6 mg (16)	12.1±4.0 mg (18)
Kruskal-Wallis-ANOVA	$H_{(2,72)}=10.3$, $p<0.01$	$H_{(2,87)}=7.7$, $p<0.05$	$H_{(2,69)}=12.1$, $p<0.005$

b) comparison of ant body mass

	Long fragments	Double fragments	Short fragments
First vs. Single	$H_{(1,47)}=5.8$, $p<0.05$	$H_{(1,51)}=1.4$, n.s.	$H_{(1,44)}=8.4$, $p<0.005$;
First vs. Last	$H_{(1,51)}=8.8$, $p<0.005$	$H_{(1,71)}=7.2$, $p<0.01$	$H_{(1,51)}=8.8$, $p<0.005$
Single vs. Last	$H_{(1,46)}=0.3$, n.s.	$H_{(1,52)}=1.8$, n.s.	$H_{(1,43)}=0.002$, n.s.

Task-partitioning in the leaf-cutting ant *Acromyrmex lundi*

What triggers load transfers?

Summary. The leaf-cutting ant *Acromyrmex lundi* showed a two-stage foraging strategy. First, cutting and carrying were labours performed by different worker groups. Neither ant nor load size differed between cutters and carriers and thus could not be responsible. Along the trail, transport was a partitioned task by forming bucket brigades, i.e. several carriers transported a load consecutively. Load transfers were mainly direct; in roughly one-fourth of the observations loads were dropped on the trail. Most transfers occurred when ants passed from a new (and thus pheromone-free) trail segment to a main trail segment. Absence of trail pheromones prevented load transfers. Our data indicate that transfers were not triggered by the availability of unladen workers which could take over the load. Instead direct transfers were initiated by the laden worker.

Introduction

Ant societies are notable for the sophisticated organisation of their workforce (e.g. Hölldobler and Wilson 1990) One important topic of work organisation is task-partitioning (Jeanne 1986a), a situation when two or more workers contribute sequentially to a piece of work. A central issue in task-partitioning is the transfer of material which either can be realised directly between workers (Reyes-López and Fernández Haeger 1999), or indirectly if the material is dropped and retrieved by another worker (Fowler and Robinson 1979; Hart and Ratnieks 2000a; Hubbell *et al*. 1980).

Leaf-cutting ants use task-partitioning to an extraordinary extent in several behavioural contexts such as foraging (Fowler and Robinson 1979; Hart and Ratnieks 2000a; Hubbell *et al*. 1980), trail construction (Howard 2001) or waste management (Anderson and Ratnieks 2000; Hart and Ratnieks 2001). Task-partitioning during foraging can exist at two stages. First, harvesting can be partitioned between cutting and carrying ants. In the polymorph *Atta* species this enables a colony to allocate worker of different body sizes to specific tasks, e.g. by allocating large workers to the energy-intense cutting (Roces and Lighton 1995) and smaller workers to carrying (Röschard and Roces 2002a; Röschard and Roces 2002d). However, previous observations on *Acromyrmex lundi* revealed that a similar task-partitioning may be apparent in a much less polymorph species, indicating that additional advantages may exist. Thus in the first part of our study I analysed division of labour between cutting and carrying ants and further transfers during transport in *Acromyrmex lundi*.

Second, transport may be partitioned by forming bucket brigades, i.e. several workers transport the load consecutively (Fowler and Robinson 1979; Hubbell *et al*. 1980; Röschard and Roces 2002a). What may be the advantage of bucket brigades?

Recent studies suggested the benefit of time saving, i.e. transport by bucket brigades is faster than if one worker carries the load all the way. Travel speed of fragments transported by *A. colombica* foragers was faster after load transfer (Anderson and Jadin 2001), and transfers in the seed-harvesting ant *Messor barbarus* led to a better size-matching of worker and load (Reyes-López and Fernández Haeger 1999; Reyes-López and Fernández-Haeger 2001), thus suggesting that total travel time of fragments was reduced by bucket brigades. However, data of the grass-cutting ant *Atta vollenweideri* showed that fragments transported by a bucket brigade travel longer than fragments carried by one carrier all the way to the nest, because load transfer includes time delays both until a fragment is retrieved and the handling time of the subsequent carrier (Röschard and Roces 2002a; Röschard and Roces 2002e) thus questioning the effect of time benefit.

Possibly the primary benefit of load transfers can be found at the colony level in an enhanced information flow rather than on the level of the individual transport (Roces and Hölldobler 1994; Roces and Núñez 1993). Ants that drop their load at the main trail and return to the foraging place may easier find their way back to the source, following their freshly-deposited pheromone trail (Fowler and Robinson 1979; Hubbell *et al*. 1980) and by returning and continuing to harvest ants may reinforce the chemical trail thus enhancing recruitment to the source (Röschard and Roces 2002c; Chapter 5).

Besides the effect of recruitment, unladen workers may receive directly information by the dropped load. The more workers are involved in the transport of loads, the more will receive information about currently harvested sources and their quality. Recruited foragers preferably harvest the source their nestmates are carrying on the specific trail (Howard *et al*., 1996), hence a conditioning of foragers takes place (Roces 1990b; Roces 1994). In a similar way one could imagine that an attractive fragment on the trail may condition foragers on a specific source or enable them to choose between fragments of different quality. Interesting in this context are results of *A. vollenweideri.* Here load dropping occurred more frequently and after shorter travel distances if foragers carried a high-quality load than if it was a low-quality load (Röschard and Roces 2002c; Chapter 5). Foragers with high-quality loads might be more motivated: a) to pass on this information and b) to return to the source than foragers with low-quality sources, leading to the higher frequency of transfers and therefore to the occurrence of bucket brigades

A further advantage may be related to direct transfers. Previous observations on *Atta vollenweideri* and *Acromyrmex lundi* revealed that laden foragers had frequent interactions with unladen nestmates. The unladen workers antennated and probed the load which in some cases led to a transfer of the load. In other cases the laden foragers kept approaching unladen nestmates apparently searching for carriers to pass over its load. The frequency of interactions and the time a laden worker needs to find a “receiver ant” may give a feedback to the laden forager about the attractivity of its load (Seeley 1989b). *A. vollenweideri* foragers in the field presented with sources of different quality increased the frequency of bucket brigades while carrying high-quality loads, and decreased it while carrying low-quality loads, which strongly indicates that the occurrence of bucket brigades is regulated via feedback (Röschard and Roces 2002c; Chapter 5). As feedback seems improbable if ants drop loads, direct transfers apparently were responsible. Such a feedback would demand a sufficiently high frequency of direct transfers. However, to present most studies on bucket brigades do not distinguish between direct transfer and load dropping. The second part of our study therefore deals a) with the frequency of direct transfers and b) with the question what triggers transfers.

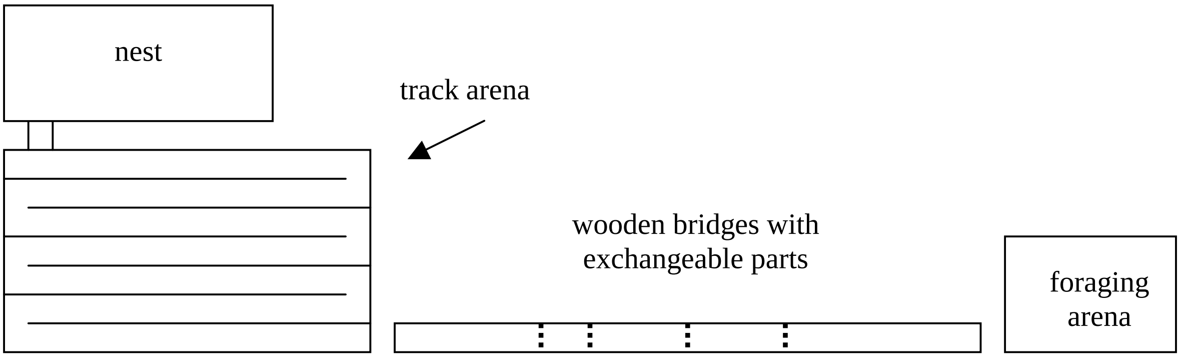
Hubbell *et al*. (1980) showed that sudden perception of trail pheromones can trigger load transfer, thus ants in the field transferred their load when reaching the main trail. (They did not distinguish between direct transfer and load dropping.) This gives rise to several questions: Does the absence of trail pheromones prevent load transfers? This would mean that ants in the field do not drop their load on faintly marked side trails. How frequent are direct transfers? Who initiates a direct transfer? Does the availability of unladen nestmates that could take over a load trigger a transfer? Or are load transfers an effect of distance, i.e. do ants transfer their loads after they carried it a certain distance irrespective of trail marking or ant density? I approached these questions with laboratory experiments on *Acromyrmex lundi.* Ants were allowed to forage on a trail of which trail segments easily could be exchanged. Ants were presented with either new and thus pheromone-free segments or main trail segments. The frequency of transfers was measured (i) on the exchanged segments, and (ii) after them, when ants reached the main trail again,. Inserted segments had different length, in order to investigate the distance effect. I analyse the percentage of direct transfers and discuss, based on our data, the effect of the presence of unladen nestmates on the initiation of direct transfers.

Material and Methods

Studies were conducted in December 2000 and July 2001 on a laboratory colony of *Acromyrmex lundi* at the University of Würzburg. Colonies were kept in plastic chambers (20 x 20 x 15 cm) connected with plastic tubes. In order to achieve sufficiently long trail lengths, one of these chambers was connected with a track arena, i.e. a box of 0.5 x 2 m in which small partition walls divided the space into approx. 7 cm wide trails which were connected on alternating sides. Therefore ants had to walk each two meters a 180° turn around a partition wall to the next trail section. Ants were allowed to accustom themselves to this set-up for one day prior to the experiments. Then, the track arena was connected with foraging arenas.

In order to study task partitioning between cutting and carrying, the track arena was connected with a plastic tube with a foraging arena of 20 x 20 x 15 cm where ants were fed ad libitum with *Ligustrum vulgaris*. Harvesting was observed by following fragments from the cutting on for the next four metres of the trail. Once a fragment passed the four metres mark, it was regarded as being carried to the nest. All involved ants (cutters as well as carriers) were caught afterwards, and ants and loads were weight to the nearest 0.1 mg. In addition, the distance each fragment was carried by a worker was measured.

In order to investigate the effect of trail pheromones on the occurrence of load transfers, the track and foraging arena were connected by wooden bridges of a total of 2.90 m length. Ants were allowed to move freely in the track arena for the whole time of the experiment. On the wooden bridges, however, they only were allowed to forage during daytime for the hours of the experiment, then they were set back to the nest. The bridges contained several segments which could be exchanged rapidly. During an assay one segment was carefully removed and a new segment of the same length was inserted which had not been used by the ants before and thus was completely free of trail pheromones. During the following 10 minutes I counted how many ants dropped their load *on* the inserted segment and on a 30 cm section *after* it, respectively. Length of the inserted segment was 20, 60 or 100 cm. Control consisted in carefully removing a main trail segment of 20, 60 or 100 cm length and inserting it again. Order of the segments was randomised, and with each segment type 16 tests were done.



Results

Task partitioning between cutting and carrying

Only 38 % of the cutters (18 ants) carried their fragment more than 4 m and thus probably to the nest (Fig. 1). Most cutters transferred their fragments directly at the cutting site (37%, 19 ants) and 24% (12 ants) carried it for a short distance. Thus, foraging *Acromyrmex lundi* showed a clear division of labour between cutting and carrying. In those cases the cutter dropped the load, transport mostly was performed by one f0urther forager (46 % of all observations, 23 fragments).

16% (8) loads were transferred once more to a third nestmate, so that workers carried the fragment consecutively by forming a bucket brigade (Fig. 1). At the cutting site, fragments were dropped, direct transfers were not observed. On the trail in contrast, fragments generally were transferred directly between nestmates.

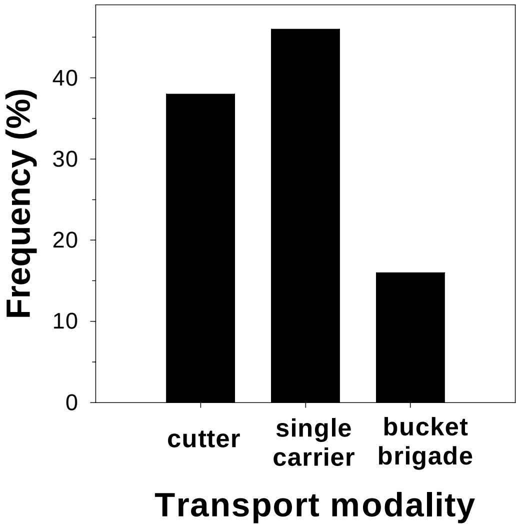


Fig. 1:
Transport of fragments to the nest. Fragments were transported either by the cutter itself, by a single carrier, i.e. the cutter dropped the fragment and a nestmate retrieved it, or by a bucket brigade. Bucket brigades consisted of the cutting ant and two further foragers which transported the load consecutively. Trail length was 14 metres, ants were harvesting ad libitum on *Ligustrum vulgaris.* Load transport was observed from the harvesting place for four metres; ants walking further were regarded as walking to the nest.

Note that the term “transfer” refers to both direct and indirect transfers. “Cutter” I call an ant which cut a fragment, irrespective of whether or how far it carried it afterwards. “Carrier” always refers to ants which retrieved a fragment they did not cut previously.

There was no size difference between cutters that carried their fragment to the nest, cutters which dropped it and carriers (Median, Quartile range: (cutters-nest) 4.8 mg, 1.7 mg, n=18; (cutters-drop) 4.3 mg, 1.5 mg, n=31; (carriers) 4.9 mg, 2.1 mg, n=40; Kruskal-Wallis-Test: $H_{(2, 89)}=1.2$, p=0.5, NS). Neither differed load mass between these groups (Median, Quartile range: (nest) 3.0 mg, 3.7 mg, n=18; (drop) 5.0 mg, 3.4 mg, n=31; (carriers) 5.15 mg, 3.2 mg, n=40; Kruskal-Wallis-Test: $H_{(2, 89)}=5.2$, p=0.08, NS). Load mass correlated significantly with body mass of cutters but not with carrier body mass (Spearman Rank Correlation Test: (cutters) t=2.88, n=49, $p<0.01$, $y=2.45+0.53x$, $r^2=0.1$; (carriers) t=0.97, n=40, p=0.3, NS). Thus load dropping was not affected by forager body mass or load mass.

Frequency of direct transfers

Percentage of direct transfers compared to all transfers (direct and load dropping) ranged from 54 to 90%, overall frequency was 73% (n=324). There was no difference in the percentage of direct transfers between an inserted trail segment of distinct length nor between marked and new trail segments (Fig. 2). Therefore I pool data for the following analyses, and the terms "transfer", "dropping" or "passing" refer to both direct and indirect transfers.

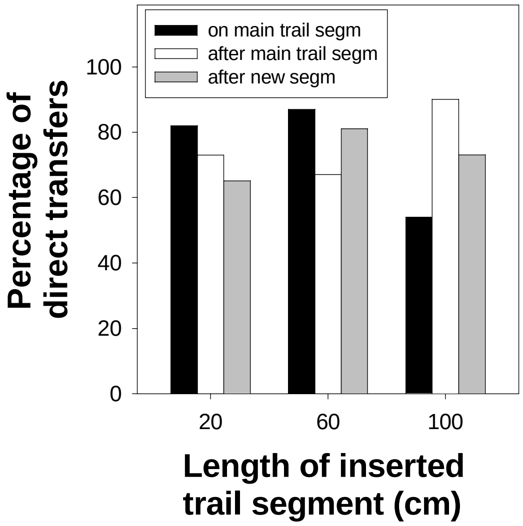


Fig. 2:
Percentage of direct transfers compared to all transfers (direct and load dropping) if transfer occurred on a main trail segment, after a main trail segment or after a new segment (see text). Frequency ranged from 54 to 90%, overall frequency amounted to 73% (n=324). Transfers on new trail segments were not included as only 1 (60 and 100 cm) or 3 (20 cm) loads were transferred.

Effect of trail pheromones

I investigated the effect of trail pheromones on the occurrence of bucket brigades by inserting either trail segments which were absolutely new (thus without any trail pheromone) or which were main trail segments and thus probably marked by the ants. I measured load transfer *on* the segment as well as load dropping on the 30 cm section *after* it.

First I consider transfers on the inserted segment, for investigating whether the absence of trail pheromones prevented load transfers. Frequency of load transfer was significantly lower on new than on main trail segments, irrespective of the length of the inserted trail segment (Mann-Whitney-U-Test (20 cm): U=66.5, Z=2.32, p<0.05; (60 cm) U=36.5, Z=3.45, p<0.001; (100 cm) U=62.5, Z=2.47, p<0.05). However, frequency was low even on main trail segments. Segments of different lengths did not differ in the amount of load transfers (Kruskal-Wallis-Test (main trail segments) $H_{(2, 48)}=3.4$, p=0.2; (new segments) $H_{(2, 48)}=0.6$, p=0.7) (Fig. 3a).

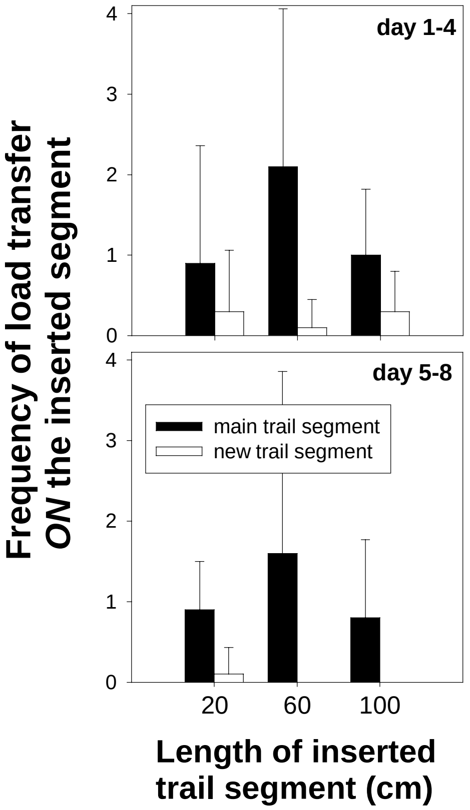


Fig. 3:
Frequency of load transfer (direct and load dropping) on the inserted segment. Black bars indicate main trail segments, grey bars new segments (n=16). Data are presented separately for the first and the second phase of the experiment, in order to detect possible time dynamics. Load transfers occurred significantly less often on new trail segments than on main trail segments, but frequency was low in both cases. Transfer frequency was not affected by the length of the inserted segment and did not change in the course of the experiment.

I then consider load transfers *after* an inserted segment, in order to investigate the effect of sudden appearance of trail pheromones. Behaviour of the ants was reversed to what I described above: Frequency of load dropping was much higher after new segments than after main trail segments with the exception of the 20 cm segment, where there was a slight but no significant difference (Mann-Whitney U-Test: (20 cm) U=81.5, Z=-1.8, p=0.08; (60 cm) U=56.0, Z=-2.7, $p<0.01$; (100 cm) U=32.0, Z=-3.6, $p<0.005$). Again there was no difference between segments of different lengths neither for new nor for main trail segments (Kruskal-Wallis-Test: (main) $H_{(2, 48)}=3.2$, p=0.2, NS; (new) $H_{(2, 48)}=0.1$, p=0.9, NS) (Fig. 4a).

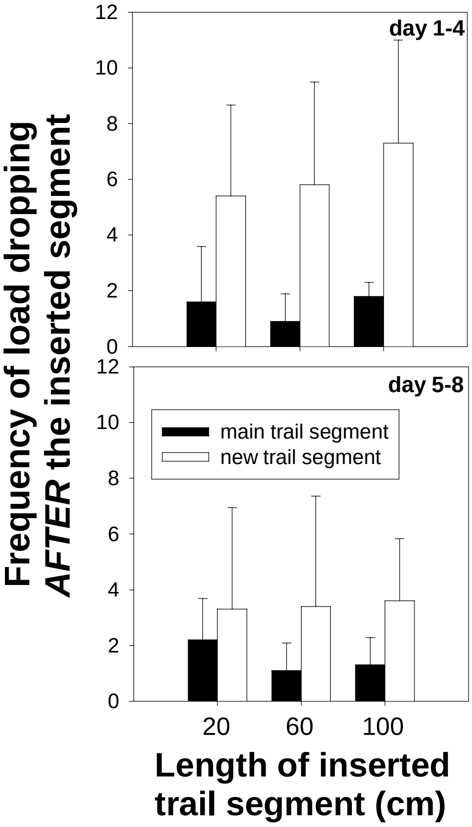


Fig. 4:
Frequency of load transfer after the inserted segment Black bars indicate main trail segments, grey bars new segments (n=16). Load transfers occurred significantly more often on new trail segments than on main trail segments. Note the different scale on the y-axes of Fig. 3 and 4. Frequency of transfer after main trail segments did not change in the course of the experiment, but frequency after new trail segments declined significantly in the second phase of the experiment. Length of the inserted segment did not affect frequency of transfers.

Effect of forager density

In order to analyse the effect of forager density, i.e. the availability of unladen workers which could take over a load, I compared frequency of load transfers *after* and *on* an inserted main trail segment. For exchanging the trail segments the trail briefly had to be interrupted. Thus some ants queued on both sides of the trail. After inserting the segment again, for a short time a higher density of ants was abundant on the inserted segment than after it. The frequency of transfers, however, did not differ after and on an inserted main trail segment (Mann-Whitney U-Test: U=917.0, Z=-1.7, p=0.09; NS). I can conclude therefore that ant density did not trigger load transfers.

Dynamics of load transfer

In order to analyse the dynamics in load transfer during the time of the experiment, frequency of transfers during the first four experimental days were compared with the frequency of day 5 to 8. Considering load transfers on the inserted segment, there was no significant difference (Mann-Whitney U-Test: (main trail segments) U=245.0, Z=0.6, p=0.5, NS; (new segments) U=241.0, Z=0.7, p=0.5, NS; data were pooled, because load lengths did not differ). However, if I now consider load transfers after a segment load dropping occurred significantly more often on the first four than on the consecutive four experimental days (Mann-Whitney U-Test: (main) U=231.0, Z=-0.9, p=0.3, NS; (new) U=156.0, Z=2.5, p<0.01). Thus, the “main trail effect”, that load transfers were triggered by sudden appearance of trail pheromones declined. At the same time ants began to drop fragments when they entered the track arena. As activity was very high in the track box, it was impossible to count all load droppings as it was done on the wooden trail. Therefore, I observed 30 ants when they entered the track box for a distance of 30 cm or until they dropped the load. 59±15% of the observed ants dropped their load when entering the track box (n=4 observation series of 30 ants each). Thus, ants continued to transfer their loads to nestmates but the place where this was done changed in the course of the experiment.

Discussion

Acromyrmex lundi showed a clear division of labour during foraging. In a first stage, cutting and carrying were performed by different worker groups, in a second stage load transfers occurred during transport on the trail, in particular when passing from a new trail sector to the main trail.

Partitioning of cutting and carrying was shown for several *Attini* such as *Atta sexdens* (Fowler and Robinson 1979), *A. cephalotes* (Hubbell *et al*. 1980) and *A. vollenweideri* (Röschard and Roces 2002a; Röschard and Roces 2002e). This similar pattern might have evolved because of rather different constraints. In *A. sexdens* and *A. cephalotes*, a group of arboreal cutters cuts leaf stems and drops them to ground, where nestmates cut them into transportable fragments and carry them to the nest. Thus, a colony can save dozens of trips up and down the tree, saving foraging time and energy. *A. vollenweideri* in contrast cuts grass blades, hence, by dropping a fragment hardly any foraging time or energy can be saved. The advantage for the colony in this species rather may be the allocation of larger workers to cutting and smaller ones to carrying (Röschard and Roces 2002a; Röschard and Roces 2002d). Cutting is an energetically extremely intense procedure with metabolic rates 30 times higher than during resting (Roces and Lighton 1995) whereas carrying can be time consuming because of the long foraging trails (Lewis *et al*. 1974; Weber 1972), but it is much less energy consuming than cutting (Lighton *et al*. 1987; Roces and Lighton 1995). *A. vollenweideri* seems to respond to the energetic demand of cutting and time demand of carrying by assigning large workers to the energy-intensive and small workers to the time-intensive activity. In our experimental set-up no foraging time was saved by *Ac. lundi* cutters dropping their fragments. In a natural context when ants harvest on bushes or trees this might be a relevant aspect but up to present there are no reports of such a behaviour of a *Acromyrmex* species in the field. Also *Acromyrmex lundi* did not show an allocation in size distribution of workers in our experiment. Because of the less marked size polymorphism of the workers this also was expected to be much less likely. This may indicate further hitherto not investigated effects of task-partitioning like the increased experience if workers are specialised or the need to monopolise the harvested plant.

Beside the transfer between cutter and carrier a second transfer occurred during transport. Approximately each fifth load was transferred a second time from carrier to carrier, thus forming bucket brigades. I only observed the first four meters of the trail thus possibly some transfers occurred later, so that the exact percentage could be a bit higher. However, our data correspond exactly to data recently published for *A. vollenweideri* which showed that on a trail of 10 m length bucket brigades occurred in 16% of all transports (Röschard and Roces 2002c; Chapter 4). Transfers in bucket brigades in most cases were direct thus I can exclude that loads were dropped because they were not sufficiently attractive and therefore rejected. Similarly I can exclude load carriage effects, i.e. that a load was too big for an ant to be carried, as neither load nor ant mass differed between bucket brigades and single carrier, i.e. a carrier which performs all the transport to the nest.

So what could be the advantage of a bucket brigade? In social insects as well as in human societies, bucket brigades may serve for an increased turnover of material or in other words for a decrease in foraging or working time (Bartholdi *et al*. 2001; Jeanne 1986b; Reyes-López and Fernández Haeger 1999) and because this probably is the most intuitively expected benefit, it was proposed for a number of further transport chain systems (Anderson and Jadin 2001; Fowler and Robinson 1979; Hubbell *et al*. 1980; López *et al*. 2000). I did not measure total transport time of loads carried by bucket brigades or by one carrier, therefore I do not know whether this may be relevant to *Acromyrmex lundi*. However, it seems doubtfully. Subsequent carrier were not larger than previous carrier in a bucket brigade, thus they are not expected to walk faster. Furthermore, I often observed that transfers could take up to one minute with both carriers “struggling” about who will continue the transport (unpublished observations). Thus it seems likely that bucket brigades rather increased instead of decreased travel times compared to carrier which walked all the way through.

In *Atta vollenweideri* sequential load transport in general took longer than if one ant carried the fragment all the way through (Röschard and Roces 2002a; Röschard and Roces 2002e), so that no time benefit could have promoted the occurrence of bucket brigades. Equally, load carriage effects were absent, yet food quality had a marked effect on the occurrence of bucket brigades: High-quality loads were transferred more often and after shorter distances than low-quality loads. The authors suggest that the crucial advantage of bucket brigades is related to an enhanced information transfer (see also Roces and Hölldobler 1994; Roces and Núñez 1993). This could take place in three ways: First, after transferring their load on the main trail carriers returned to the previous foraging place which was located on a side trail and continued foraging. These ants a) might easier find the source again following their freshly-deposited pheromone trail back and b) will travel more frequently on that particular trail or patch section than if it walked all the way to the nest. Thus, trail marking between the food source being exploited and the main trail could be enhanced to a much larger extent, leading to a quicker recruitment as well as a faster monopolisation of the discovered food source. Second, by transferring a load between several foragers information about currently harvested sources and their quality might be spread among more foragers. This may enable workers in their subsequent foraging trip to search specifically for the high-quality source. Third, the transferring forager may receive a feedback about the quality of the load it is currently carrying by the time until it can transfer the load or by the amount of foragers which approach to take it over. Thus, as in *A. vollenweideri*, the advantage of load transfer may be rather found on colony level because of an enhanced information flow than on the individual level by reducing travel time of fragments. Or in other words colony material intake may be increased through recruitment and feedback communication at the expense of reduced foraging performance of the individuals.

What triggers load transfers? Up to now little is known about possible parameters. Anderson and Jadin (2001) suggest that loads are transferred if the laden worker is not able to walk fast enough. This may happen if the load is too big for the ant to carry or the forager very small. Load transfer then would increase material intake rates at the colony level. Unfortunately this study does not give any data about load size or worker mass but only about walking velocity of laden foragers. But velocity seems an inappropriate parameter to account for the occurrence of load transfers. In our observations ants often reduced their speed before they transferred the load, thus they walked slow because they were going to transfer their load rather than they transferred because of their low speed. In addition worker intensively involved in trail marking also would be expected to walk slow thus walking speed as such not necessarily indicates that the ant is not capable of walking faster. In our experiment, neither ant nor load size differed between bucket brigades and transport performed by one carrier, thus slow walking speed seems an implausible trigger.

Foragers of *Atta sexdens* and *A. cephalotes* at the beginning of a foraging cycle drop their loads when reaching the main trail (Fowler and Robinson 1979; Hubbell *et al*. 1980). The same happened if workers reached a cardboard which was lying on the main trail before and thus probably was strongly impregnated with trail pheromones (Hubbell *et al*. 1980). The authors conclude that trail pheromones of the main trail triggered the dropping. Our results support this and add the complementary view. Load transfers mostly occurred if a forager passed from a new and therefore unmarked trail sector to the main trail. On the new segment in contrast where chemical marking was absent nearly no fragments were transferred, thus lack of pheromones prevented load dropping.

The study of Hubbell *et al*. (1980) leaves open whether loads were transferred directly or indirectly, i.e. that the ant dropped the load. By direct transfer of loads, however, foragers may receive a direct feedback about quality of their load as well as the general need of the colony for material. Feedback parameters could be the time delay until a nestmate is found to pass the load. Therefore I performed our experiments with the additional consideration of the type of transfer. I found that the large majority of loads were transferred directly. This was independent of the location of the transfer, i.e. whether it happened on or after an inserted segment. The percentage of direct transfers compared to all transfers also was independent of the presence of trail pheromones. This means that as described above for all transfers, most direct transfers occurred when the ant passed from a new trail sector to the main trail.

Thus, when reaching the main trail most ants did not drop the load but passed it over to a nestmate. This implies that the laden forager initiated the transfer although I do not have exact evidence. I often observed that the laden carrier reduced its walking speed and moved very slowly until a nestmate approached and took the load, or it kept approaching unladen nestmates coming from the nest whereby it rather meandered along the trail instead of walking straight ahead. As most direct transfers occurred after reaching the main trail this indicates that the laden forager initiates the transfer, as the laden foragers perceived that it passed from a new to a main trail sector, whereas the subsequent unladen foragers did not have any information about that.

Another trigger – especially if most transfers occur direct – could be the availability of nestmates to pass over the load. In this case, transfer frequency should increase with increasing density of unladen foragers. For exchanging the segments, the trail had to be interrupted briefly. Thus on both sides some ants queued which could not continue walking. After inserting a segment ant density for a short time was higher than on the trail segment beside the inserted one. Hence, on main trail segments where the effect of sudden appearance of trail pheromones was absent, I would expect an increase in transfers on the inserted segment. This was not the case, I therefore have no hints that forager density may trigger load transfer.

Ants changed the location of the transfers during the experiment. During the last days frequency of transfers after new segments (thus at the location where transfers mainly occurred) declined. Instead, ants dropped their load when entering the track box building up a pile. Ants were allowed to move in the track box all the time, but on the wooden bridges only for the hours of the experiment. Thus it may be that eventually the track arena regarded by the ants as main trail, may be because it was stronger scented chemically or because of visual cues or because of a positive feedback of the pile of leaf fragments. On the wooden bridges, where the only cue was the appearance of trail pheromones, less and less load transfers occurred.

The role of a further possible trigger keeps unresolved at this stage. Above I discussed that the time delay until a load can be passed as well as interactions between laden and unladen foragers may give a feedback to the laden forager about the attractivity of its load. In addition, I frequently observed intense interactions between laden and unladen workers with the unladen worker biting into the fragment and tearing it. In some cases this led to a transfer, in others the unladen forager continued running towards the patch. The frequency as well as the intensity of these interactions may be a further cue by which laden foragers receive a feedback about the quality of their load. Further experiments dealing with this issue could shed light on the mechanism that triggers load transfers.

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Summary

This study investigates the foraging behaviour of grass-cutting ants, *Atta vollenweideri*, with specific consideration of the following issues: (a) cutting behaviour and the determination of fragment size, (b) the effect of load size on transport economics, (c) division of labour and task-partitioning.

Grass-cutting ants, *Atta vollenweideri*, harvest grass fragments that serve as substrate for the cultivation of a symbiotic fungus. Foragers were observed to cut grass fragments across the blade, thus resulting in longish, rectangular-shaped fragments in contrast to the semicircular fragments of leaf-cutting ants. Cutting was very time-consuming: In tough grasses like the typical grassland species *Paspallum intermedium* and *Cyperus entrerrianus*, cutting times lasted up to more than 20 minutes per fragment and roughly half of all initiated cutting attempts were given up by the ants. Foragers harvesting the softer grass *Leersia hexandra* were smaller than those foraging on the hard grasses.

Fragment size determination and the extent of size-matching between ant body size and fragment size was investigated regarding possible effects of tissue toughness on decision-making and as a function of the distance from the nest. Tissue toughness affected decision-making such that fragment width correlated with ant body mass for the hard grass but not for the soft one, suggesting that when cutting is difficult, larger ants tend to select wider grasses to initiate cutting. The length of the fragments cut out of the two grass species differed statistically, but showed a large overlap in their distribution. Distance from the nest affected load size as well as the extent of size-matching: Fragments collected directly after cutting were significantly larger than those carried on the trail. This indicates that fragments were cut once again on their way to the nest. Size-matching depended on the trail sector considered, and was stronger in ants sampled closer to the nest, suggesting that carriers either cut fragments in sizes corresponding to their body mass prior transport, or transferred them to nestmates of different size after a short carrying distance.

During transport, a worker takes a fragment with its mandibles at one end and carries it in a more or less vertical position. Thus, load length might particularly affect maneuverability, because of the marked displacement of the gravitational center. Conversely, based on the energetic of cutting, workers might maximise their individual harvesting rate by cutting long grass fragments, since the longer a grass fragment, the larger is the amount of material harvested per unit cutting effort. I therefore investigated the economics of load transport by focusing on the effects of load size (mass and length) on gross material transport rate to the nest. When controlling for fragment mass, both running speed of foragers and gross material transport rate was observed to be higher for short fragments. In contrast, if fragment mass was doubled and length maintained, running speed differed according to the mass of the loads, with the heavier fragments being transported at the lower pace. For the sizes tested, heavy fragments yielded a higher transport rate in spite of the lower 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. The sizes of the fragments cut by grass-cutting ants under

natural conditions therefore may represent the outcome of an evolutionary trade-off between maximising harvesting rate at the cutting site and minimising the effects of fragment size on material transport rates.

I investigated division of labour and task partitioning during foraging by recording the behaviour of marked ants while cutting, and by monitoring the transport of fragments from the cutting until they reached the nest. *A. vollenweideri* foragers showed division of labour between cutting and carrying, with larger workers cutting the fragments, and smaller ones transporting them. This division was absent for food sources very close to the nest, when no physical trail was present. Along the trail, the transport of fragment was a partitioned task, i.e., workers formed bucket brigades composed of 2 to 5 carriers. This sequential load transport occurred more often on long than on short trails. The first carriers of a bucket brigade covered only short distances before dropping their fragments, turned back and continued foraging at the same food source. The last carriers covered the longest distance. There was no particular location on the trail for load dropping , i.e., fragments were not cached.

I tested the predictions of two hypotheses about the causes of bucket brigades: First, bucket brigades might occur because of load-carriage effects: A load that is too big for an ant to be carried is dropped and carried further by nestmates. Second, fragments carried by bucket brigades might reach the nest quicker than if they are transported by a single carrier. Third, bucket brigades might enhance information flow among foragers: By transferring the load a worker may return earlier back to the foraging site and be able to reinforce the chemical trail, thus recruitment. In addition, the dropped fragment itself may contain information for unladen foragers about currently harvested sources and may enable them to choose between sources of different quality. I investigated load-carriage effects and possible time-saving by presenting ants with fragments of different but defined sizes. Load size did not affect frequency of load dropping nor the distance the first carrier covered before dropping, and transport time by bucket brigades was significantly longer than by single carriers. In order to study the information transfer hypothesis, I presented ants with fragments of different attractivity but constant size. Ants carrying high-quality fragments would be expected to drop them more often than workers transporting low-quality fragments, thus increasing the frequency of bucket brigades. My results show that increasing load quality increased the frequency of bucket brigades as well as it decreased the carrying distance of the first carrier. In other words, more attractive loads were dropped more frequently and after a shorter distance than less attractive ones with the first carriers returning to the foraging site to continue foraging. Summing up, neither load-carriage effects nor time-saving caused the occurrence of bucket brigades. Rather, the benefit might be found at colony level in an enhanced information flow.

Zusammenfassung

Die vorliegende Dissertation untersucht das Sammelverhalten der grasschneidenden Ameise *Atta vollenweideri*, unter besonderer Berücksichtigung der folgenden Themen: (a) das Schneideverhalten und die Wahl der Fragmentgröße, (b) der Effekt der Fragmentgröße auf den Transport und (c) die Arbeitsteilung während des Sammelns.

Die Grasschneiderameise *Atta vollenweideri* sammelt Grasfragmente, die im Nest zerkleinert werden, um darauf einen symbiotischen Pilz zu züchten. Die Sammlerinnen schnitten ihre Fragmente quer über die Halmbreite, so dass längliche, rechteckige Fragmente entstehen, im Gegensatz zu den halbkreisförmigen Fragmenten der Blattschneiderameisen. Das Schneiden war ein sehr zeitaufwendiger Prozess: Bei harten Gräsern wie die für die Savanne typischen *Paspallum intermedium* und *Cyperus entrerrianus* betrug die Schneidezeit pro Fragment bis zu 20 Minuten oder länger. Etwa die Hälfte aller begonnenen Schnitte wurde von den Ameisen aufgegeben. Sammlerinnen, die das weichere Gras *Leersia hexandra* ernteten, waren kleiner als diejenigen, die die harten Gräser schnitten.

Ich untersuchte, inwiefern die Härte des geschnittenen Materials und die Entfernung vom Nest einen Einfluss auf die Wahl der Fragmentgröße und auf die Stärke der Korrelation zwischen Ameisen- und Fragmentgröße hat. Die Länge „harter“ und „weicher“ Fragmente unterschied sich zwar statistisch, zeigte aber eine starke Überlappung. Die Korrelation zwischen Ameisen- und Fragmentgröße existierte bei dem harten Gras, nicht jedoch bei dem weichen Gras. Das heißt, dann wenn das Schneiden schwierig wird, suchen sich größere Tiere breitere Halme zum Schneiden (bzw. kleinere Tiere schmalere Halme). Sowohl Fragmentgröße als auch die Stärke der Korrelation zwischen Fragment- und Ameisengewicht hing von der Entfernung zum Nest ab: Fragmente, die ich direkt nach dem Schneiden sammelte, waren signifikant größer als solche, die ich auf dem Trail sammelte. Dies bedeutet, dass die Fragmente auf ihrem Weg zum Nest ein zweites Mal geschnitten wurden. Die Korrelation zwischen Fragment- und Ameisengewicht war um so stärker, je näher am Nest die Tiere gesammelt wurden, was bedeutet, dass die Trägerinnen entweder die Fragmente vor dem Transport entsprechend ihrer eigenen Körpergröße geschnitten hatten, oder aber dass die Fragmente nach einer kurzen Strecke an Nestgenossinnen anderer Körpergröße übergeben wurden.

Um ein Fragment zu transportieren, packen *A. vollenweideri*-Arbeiterinnen das Fragment mit den Mandibeln an einem Ende und halten es mehr oder weniger senkrecht. Daher ist zu vermuten, dass lange Fragmente schwieriger zu manövrieren sind, da sich der Schwerpunkt mit zunehmender Länge nach oben verschiebt. Lange Fragmente haben jedoch den Vorteil, dass die Menge an geerntetem Material pro Schneideversuch größer ist als bei kurzen; Arbeiterinnen könnten also ihre Sammelrate jedoch dadurch maximieren, dass sie möglichst lange Fragmente schneiden. Im Hinblick auf die Schneidekosten wären dann also lange Fragmente vorteilhaft, im Hinblick auf den Transport hingegen kurze. Ich untersuchte daher den Effekt der Fragmentgröße (Länge und Gewicht) auf den Transport.

Waren die Fragmente gleich schwer aber unterschiedlich lang, war die Laufgeschwindigkeit der Arbeiterinnen und damit auch die Eintragsrate bei den kurzen Fragmenten höher. Wenn hingegen das Fragmentgewicht verdoppelt und die Länge konstant gehalten wurde, unterschied sich die Laufgeschwindigkeit entsprechend dem Gewicht der Fragmente: Schwere Fragmente wurden langsamer getragen als leichte. Die Transportrate hingegen war für die schwereren Fragmente höher, da der höhere Eintrag aufgrund des zusätzlichen Gewichts die langsamere Laufgeschwindigkeit aufwog. Die Fragmentgrößen, die Grasschneiderameisen unter natürlichen Bedingungen schneiden, könnten daher im Laufe der Evolution aufgrund des Kompromisses entstanden sein, einerseits die Ernterate am Schneideort zu maximieren und andrerseits die negativen Effekten der Fragmentgröße auf den Transport möglichst gering zu halten.

Ich untersuchte die Arbeitsteilung während des Sammelns, indem ich das Verhalten schneidender Tiere beobachtete und indem ich den Fragmenttransport vom Schneideplatz bis zum Nest verfolgte. Schneiden und Tragen von Fragmenten wurde von unterschiedlichen Arbeiterinnengruppen durchgeführt, wobei größere Sammlerinnen die Fragmente schnitten und kleinere sie transportierten. Diese Arbeitsteilung existierte nicht, wenn die Futterquelle sehr nah war, wenn also kein sichtbarer Trail vorhanden war. Der Transport selbst war ebenfalls unterteilt: Die Trägerinnen bildeten Arbeitsketten, die aus zwei bis fünf Trägerinnen bestanden. Diese Arbeitsketten kamen häufiger auf langen als auf kurzen Trails vor. Die ersten Trägerinnen einer solchen Arbeitskette legten nur eine kurze Strecke zurück, bevor sie das Fragment ablegten oder an eine Nestgenossin abgaben. Sie kehrten dann zur gleichen Futterquelle zurück und sammelten weiter. Die letzten Trägerinnen einer Arbeitskette transportierten die Fragmente über die größte Strecke. Es gab keine speziellen Orte auf dem Trail, an denen die Fragmente abgelegt wurden.

Ich testete die Voraussagen zweier Hypothesen über den Entstehungsgrund von Arbeitsketten: Nach der ersten Hypothese könnten Arbeitsketten aufgrund von Transporteffekten entstehen, wenn z. B. ein Fragment für eine Ameise zu groß ist, daher abgelegt und von Nestgenossinnen weitergetragen wird. Fragmente könnten auch durch Arbeitsketten schneller transportiert werden, als wenn ein Tier die ganze Strecke bis zum Nest läuft. Nach der zweiten Hypothese könnten Arbeitsketten den Informationsfluss unter den Sammlerinnen erhöhen: Indem sie ein Fragment abgibt, kann eine Sammlerin früher zum Ernteort zurückkehren, sie kann so die Trailmarkierung verstärken und Nestgenossinnen rekrutieren. Zudem könnten unbeladene Arbeiterinnen durch das abgelegte Fragment selbst darüber informiert werden, was gerade geerntet wird. Dies könnte den Sammlerinnen die Möglichkeit geben, zwischen Futterquellen unterschiedlicher Attraktivität zu wählen.

Ich untersuchte die Transporteffekte und die mögliche Zeitersparnis, indem ich Ameisen Fragmente unterschiedlicher, jedoch definierter Größe sammeln ließ. Die Fragmentgröße hatte weder einen Einfluss auf die Wahrscheinlichkeit, dass ein Fragment abgegeben wurde, noch auf die Strecke, die es vor der Abgabe getragen wurde. Die Transportzeiten waren höher für Fragmente, die durch Arbeitsketten transportiert wurden, als für solche, die ein Tier die ganze Strecke trug. Um die

Informationsfluss-Hypothese zu untersuchen, ließ ich die Ameisen Fragmente sammeln, die gleich groß jedoch unterschiedlicher Attraktivität waren. Nach dieser Hypothese würde man erwarten, dass Ameisen ihre Fragmente eher ablegen, wenn sie attraktiv sind, um dann an den Ernteort zurückzukehren, so dass Arbeitsketten häufiger bei attraktiven Fragmenten auftreten sollten als bei weniger attraktiven. Meine Ergebnisse zeigen, dass ein Anstieg in der Attraktivität der Fragmente die Häufigkeit der Arbeitsketten erhöhte und dass die Strecke, die die erste Trägerin zurücklegte, kürzer war als bei weniger attraktiven Fragmenten. Anders ausgedrückt, attraktivere Fragmente wurden häufiger und nach kürzeren Strecken abgelegt als weniger attraktive. Das bedeutet also, dass die Ursache für das Vorkommen von Arbeitsketten weder in Transporteffekten noch in einer Zeitersparnis beim Transport zu suchen ist. Es scheint vielmehr, dass der Vorteil auf Kolonieebene liegt, indem der Informationsfluss unter den Sammlerinnen erhöht wird.

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Erklärung:

Hiermit versichere ich ehrenwörtlich, dass ich die vorliegende Dissertation in allen Teilen selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Darüber hinaus erkläre ich, dass die vorliegende Dissertationsschrift weder vollständig noch in Teilen in einem anderen Prüfungsverfahren vorgelegen hat und dass ich wederbereits akademische Grade erworben noch zu erwerben versucht habe.

Würzburg, 19.03.02

Publikationsliste:

Röschard J, Roces F (2002) The effect of load length, width and mass on transport rate in the grass-cutting ant *Atta vollenweideri*. Oecologia, in press

Röschard J, Roces F (2002) Cutting behaviour and fragment-size determination in the grass-cutting ant *Atta vollenweideri*. Submitted to Ecological Entomology

Röschard J, Roces F (2002) Load size determination and size-matching in the grass-cutting ant *Atta vollenweideri* depend on distance from the nest. Submitted to Journal of Tropical Ecology

Röschard J, Roces F (2002) Cutters, carriers and bucket brigades - Distance-dependent foraging strategies in the grass-cutting ant *Atta vollenweideri*. in prep.

Röschard J, Roces F (2002) Sequential load transport via bucket brigades in the grass-cutting ant *Atta vollenweideri* - Load-carriage effect or information transfer? in prep.

Röschard J, Roces F (2002) The effect of trail pheromone on the formation of bucket brigades in the leaf-cutting ant *Acromyrmex lundi*. in prep.

Tagungsbeiträge

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