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Research article

Cutters, carriers and transport chains: Distance-dependent foraging strategies in the grass-cutting ant *Atta vollenweideri*

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Summary. Most studies on leaf-cutting ant foraging examined forest species that harvest dicot leaves. We investigated division of labor and task partitioning during foraging in the grass-cutting ant *Atta vollenweideri.* Workers of this species harvest grass fragments and transport them to the nest for distances up to 150 m along well-established trunk trails. We recorded the behavior of foraging ants while cutting and monitored the transport of individually-marked fragments from the cutting site until they reached the nest. *A. vollenweideri* foragers showed division of labor between cutting and carrying, with larger workers cutting the fragments, and smaller ones transporting them. This division was less marked when plants were located very close to the nest and no physical trail was present, i.e., the cutter often transported its own fragment back to the nest. On long foraging trails, the transport of fragments was a partitioned task, i.e., workers formed transport chains composed of 2 to 5 carriers. This sequential load transport occurred more often on long than on short trails. The first carriers in a transport chain covered only short distances before dropping their fragments, and they were observed to turn back and revisit 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 of fragments transported by a chain was longer than for those transported by single workers all the way to the nest, i.e., sequential transport did not save foraging time. Two hypotheses concerning the possible adaptive value of transport chains are discussed. The first one argues that sequential transport may lead to an increased material transport rate compared to individual transport. The second one considers sequential transport as a way to enhance the information flow among foragers, thus leading to a quicker build-up of workers at particular harvesting places. It is suggested that rather than increasing the gross transport rate of material, transport via chains may favor the transfer of information about the kind of resource being actually harvested.

Keywords: Leaf-cutting ants, sequential load transport, communication, foraging, task partitioning, division of labor.

Introduction

Social insects have developed a variety of strategies for food retrieval often involving a high degree of co-operation and co-ordination. In many species, prey items that cannot be managed by single workers are retrieved co-operatively (Sudd, 1965; Franks, 1989; Anderson and Franks, 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, social insects show a sequential co-operation in which a food item or building material is passed consecutively from one worker to the next from the source to its final destination in the nest. Sequential co-operation may lead to a decreased energy and time investment during foraging (Jeanne, 1986a; Anderson and Ratnieks, 1999; Reyes-López and Fernández Haeger, 1999). It may also lead to an increase in foraging risks in the case the transfers are associated with long delays. 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, 1989).

A sequential transport of collected material implies that the task is partitioned among different workers and linked by material transfer. Task partitioning can be defined as a process in which *one* task is split up between different worker groups, in contrast to division of labor in which *different* tasks are performed by different worker groups (Jeanne, 1986a; 1986b; Ratnieks and Anderson, 1999; Anderson et al., 2002). Leaf-cutting ants of the tribe Attini show both

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division of labor (Weber, 1972; Wilson, 1980) and task partitioning to an extraordinary extent (recently reviewed by Hart et al., 2002), including different contexts such as foraging (Fowler and Robinson, 1979; Hubbell et al., 1980; Hart and Ratnieks, 2000; Hart and Ratnieks, 2001a), trail construction (Howard, 2001), or waste management (Anderson and Ratnieks, 2000; Hart and Ratnieks, 2001b).

Sequential co-operation in foraging leaf-cutting ants was first investigated in *Atta sexdens rubropilosa* and *A. cephalotes* (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, transportable 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, leaf-cutting ants show division of labor between cutters and carriers, and task partitioning during leaf transport. Cutters and carriers seem to be specialised as body size differs among them, and arboreal cutters were not seen carrying fragments back to the nest. During transport, task partitioning was also recently reported in *A. colombica* (Anderson and Jadin, 2001; Hart and Ratnieks, 2001a), 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 cut grass fragments (Jonkman, 1976), so that the whole harvesting process from the source to the nest occurs on the ground and can be directly monitored and experimentally manipulated. Observations on *Atta vollenweideri* foragers 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 (Röschard and Roces, 2003). The aim of the present study was to investigate division of labor, task partitioning and the occurrence of transport chains in foraging grass-cutting ants, *Atta vollenweideri*. In the field, size-related division of labor was addressed by measuring body size of cutting and carrying workers. The occurrence of sequential transport of grass fragments was quantified by following marked grass fragments all their way to the nest, and by recording when, where and how material was transferred among foragers. Experiments were performed on trails of different length in order to elucidate the effect of foraging distance on the occurrence of transport chains.

Material and methods

Ethogram of cutters

Field experiments were performed in the National Park Río Pilcomayo in Formosa province, Chaco region of north Argentina, between November 1998 and May 1999. Observations were performed at night using red light. We observed 22 foraging ants of a mature colony by marking individuals with a small dot of Edding® paint marker 780 or liquid TippEx® while they were initiating a cut at a grass blade of *Paspalum intermedium* (Poaceae). After cutting, single ants were observed for 45 min or until they entered the nest, with the exception of two ants that were lost after 25 and 30 minutes of observation. We noted the behavior of marked ants after cutting, either dropping the fragment or carrying it towards the nest, and recorded both the time and the distance they carried their loads. As most ants cut one or maximally two fragments during the observation time, data for a total of 37 cutting events were recorded.

In a first series aimed at investigating distance effects, cutting behavior was observed at plants located at 5 m from the nest. Observations of single foraging workers were made possible by restricting a circular area of ca. 1.5 m in diameter from the nest, beside an existing trail of 35 m total length. A plastic fence of approx. 40 cm height treated with plant oil, so as to avoid escape of the ants, surrounded the 5 m trail sector and the foraging area. The original trail was connected with the enclosed sector by wooden bridges, which allowed us to control 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, so as to standardize the plants provided each experimental day and to maintain foraging distance constant.

In a separate series, foragers from a second colony were observed at a distance of 0.5 m from the nest while harvesting a *P. intermedium* plant. Cutting and transport of 15 fragments were observed. In both experiments, ant body size was determined as the maximal head width to the nearest 0.25 mm. This was made by visual comparison of the monitored ant with a template of fixed ants of known sizes, to avoid disturbance of the foraging ant. The reliability of the method was previously checked in the laboratory with workers of known head width. The method showed a probability of error that averaged 15% (n = 80).

Quantifying sequential transport of grass fragments: “Fragmentograms”

Field experiments were conducted in November and December 1999 at the biological field station of the Reserva Ecológica El Bagual in Formosa province, north Argentina, on a large mature colony of *A. vollenweideri*. 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 on a Mettler balance. The last carriers transporting the marked fragments were caught before entering the nest, and both ant and fragments were weighed as indicated above. Fragment length was determined to the nearest 0.5 mm.

Since plants naturally harvested by the ants may differ in quality and attractiveness, ants were presented with a standardized source of artificial “paper plants”. They were produced by soaking paper stripes of 15 cm 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 the main trail and the plant being actually harvested, 10 to 20 cm beside the trail. “Paper plants” were readily accepted by the ants. Two active trails of different length were chosen for the experiments, on which ants were actively harvesting fragments out of the sedge *Cyperus entrerrianus* (Cyperaceae). One trail was 10m (henceforth: “short trail”), and the other 28 m long (henceforth: “long trail”). In independent experimental series, paper plants were presented either at 10 or at 28 m. Observations were performed during the day, since the colony showed diurnal foraging.

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

Results

Cutting of grass fragments at the plant

Upon arrival at a patch, cutters usually spent up to 5 minutes walking around on the ground and searching for cutting sites. The actual harvesting process could be divided into an initial searching phase, in which ants climbed a grass bade and walked up and down, eventually moving to neighbour blades of the same plant, and a "testing" phase in which ants on a given grass blade walked very slowly, steadily probing it at the edge with the mandibles. Typically, a cutter moved to the tip of the blade and after biting into it, it walked downward again. Cutters walked up and down the upper part of the grass blade several times before they started cutting.

After finishing the cut, they were only seldom involved in the transport of fragments. When cutting fragments out of *Paspalum intermedium*, they either directly dropped most of their fragments, or carried them only until the base of the plant or the main trail. After dropping, cutters moving back to the plant occasionally picked up a dropped fragment and carried it a short distance on the trail. Thus, irrespective of whether cutters carried their own or foreign fragments, they were transported until the main trail and rarely to the nest. Transport times by loaded cutters were very variable, ranging from 25 s to 5 min for own, and from 10 s to 12 min 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 on the same area, probably reinforcing the chemical marking with pheromones.

The behavior of cutters as a function of distance

When cutting fragments out of *P. intermedium* at 0.5 m from the nest entrance, cutters carried 60% of the fragments directly to the nest (n = 15 fragments). Forty percent of the fragments were dropped (Fig. 1). When cutting at 5 m from the nest, conversely, 79% of a total of 37 fragments were either directly dropped or carried until the base of the plant. Sixteen percent of the fragments were dropped on or near the main trail, and only 5% of them were carried directly to the nest by the cutters (Fig. 1). The proportion of dropped vs. carried fragments significantly differed at the two distances (Fig. 1, Chi-square test, Yates-corrected, dropping vs. carrying; 5 m: $\chi^2 = 5.51$, $p < 0.05$; 0.5 m: $\chi^2 = 15.94$, $p < 0.001$). Cutters dropped all their loads, i.e., no direct fragment transfers to other workers occurred.

As observed when cutting *Paspalum* fragments, most workers harvesting "paper plants" at distances of 10 and 28 m dropped or carried the pieces only a short distance: 51% and 31% of the fragments, respectively (n = 27 for the 10 m-train; n = 32 for the 28 m-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.

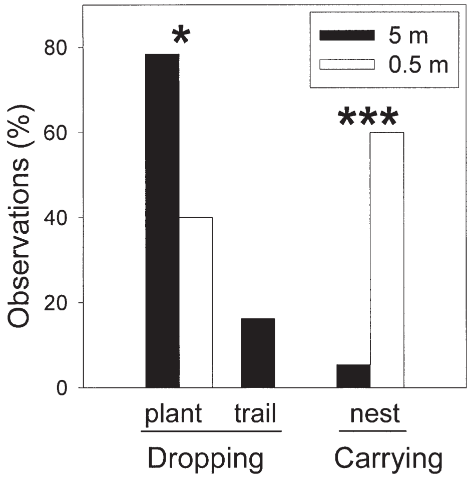

Figure 1. Behavior of cutters after cutting a fragment as a function of the distance from the nest. Cutters dropped their fragments immediately after cutting ("plant"), or carried them either to the main trail ("trail"), or to the nest. The harvested *Paspalum* plants were located either at 5 m (black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

Trail length did not influence the probability of dropping a fragment directly after cutting (Chi-Square-Test: $\chi^2 = 0.37$, $p = 0.5$). However, the probability of carrying a fragment directly to the nest significantly depended on distance: More loaded cutters reached the nest on the short than on the long trail (Fig. 2, 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.

Cutters were significantly larger than carriers on both the short and the long trail (short trail: Median, Interquartile 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 are defined as those workers that picked up and transported a fragment that they did not cut.

Fragment dropping by cutters: effects of load and body size

The question arises of what motivates a cutter to drop its fragment. We investigated the effects of both body and fragment size on the probability of dropping a fragment. 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. Fragment length significantly affects maneuverability and transport speed, because of the marked displacement of the center of gravity (Röschard and Roces, 2002). Therefore, the effects of fragment size were separately analysed by considering frag-

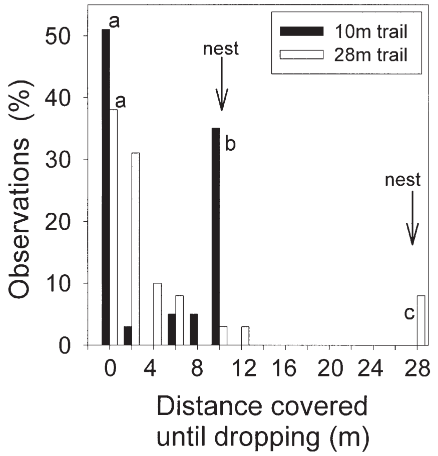

Figure 2. Transport distance covered by cutters until dropping, after cutting a fragment out of a "paper plant" at two different distances from the nest. Bars at "0 m" refer to fragment dropping immediately after cutting. The black bar at 10 m and the white bar at 28 m show the number of fragment carried directly to the nest. Trails differed in the probability that a loaded cutter reaches the nest (bars marked with "b" and "c"), but not in the probability of fragment dropping immediately after cutting (bars marked with "a"). See text for statistics.

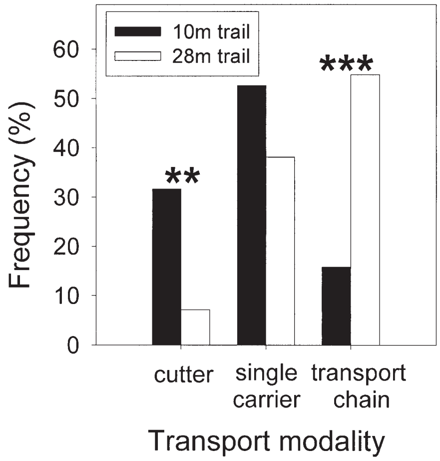

Figure 3. Modality of load transport as a function of foraging distance. On the long trail, significant more transport chains occurred than on the short trail. See text for statistics.

ment mass as well as fragment length. Based on the number of data, different statistical analyses were used for the 10 and the 28 m trail. For the short trail, average body and fragment 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 fragment size was analysed.

On the short trail, both fragment-carrying and fragment-dropping cutters had similar body masses (Median, Interquartile 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). The fragments carried by them were also similar in both mass and length (fragment 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; fragment 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). On the long trail, there was no significant relationship between transport distance of cutters and either their body mass (y = 16.5 – 0.58x, r = –0.23, n = 21, p = 0.3, NS), or the fragment mass (y = 7.29 + 0.64x, r = 0.39, n = 22, p = 0.08, NS), or the fragment length (y = 21.5 + 0.82x, r = 0.28, n = 22, p = 0.2, NS). Hence, the probability of fragment dropping does not correlate with ant size or fragment size.

Task partitioning: transport chains

Three different modalities for the transport of fragments along the trail were observed. First, a cutter carries the fragment directly to the nest, as described above. Second, fragments put down on the trail by carriers, or directly transferred, 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 "transport chain". Following our definition of "carriers", a transport chain with 2 carriers implies that a total of 3 ants are involved, i.e., a cutter plus 2 carriers.

When harvesting the artificial paper plants, transport chains were often observed along both the short and the long trail. The frequency of occurrence of transport chains significantly depended on trail distance. On the long trail, 55% of the fragments were transported by transport chains, and only 16% on the short trail (Fig. 3, Chi-Square test: $\chi^2 = 13.11$, n = 37, p < 0.001). Fifty percent of the transport chains were composed by 2 carriers, 32% by 3 carriers, and 18% by 4 or 5 carriers. Regarding the other transport modalities, cutters transported their fragments directly to the nest significantly more often on the short than on the long trail (Fig. 3). Transport by single carriers, conversely, was independent of foraging distance, averaging 53% and 38% on the short and long trail, respectively (Fig. 3).

With regard to the mode of leaf transfer, only 12.5% and 11.5% of the fragments (n = 37) were transferred directly on the short and long trail, respectively. Therefore, most fragments were dropped on the ground and collected by outgoing workers that turned back and returned to the nest. Fragments were dropped in the middle of the trail. Workers neither prefer certain places on the trail for dropping fragments, nor did they build up piles at a given location (see also Fig. 2 for dropping behavior of cutters).

Transport chains: carrying times, delays and distances

Fragments dropped on the trail attracted unladen foragers and were readily collected. 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 reg-

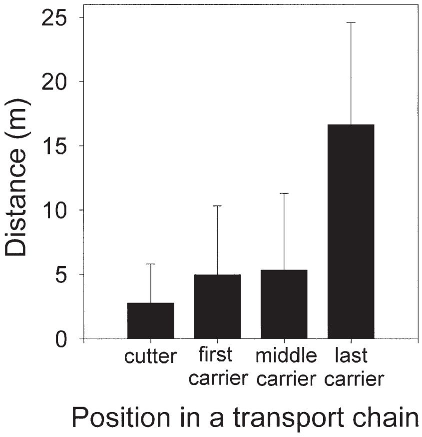

Figure 4. Transport distances of cutters, first, middle and last carriers in a transport chain, on the 28 m trail.

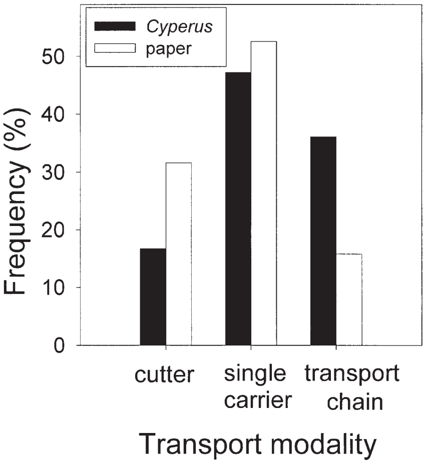

Figure 5. Modality of load transport for both natural fragments of *Cyperus entrerrianus* and fragments cut out of "paper plants" (data from Fig. 3), at 10 m from the nest.

ularly touched fragments with their gaster tips while laying them down or taking them up. 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 behavior 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.

On the long trail, the median "waiting time" of a dropped paper fragment before it was collected by a worker was 2 min. This time also includes the handling time spent by the carrier when picking up the fragment, which ranged from 5 to 30 s. Interestingly, the transport time of fragments carried by a transport chain was significantly longer, in average 8 min longer, than that of fragments carried by a single carrier (Median, Interquartile range; transport chain: 36 min, 12, n = 20; single carrier: 28 min, 9.5, n = 14, U = 72, Z = 2.4, $p < 0.05$).

The distances covered by the participants of a transport chain were very different (Fig. 4). The first carriers usually covered only a short distance of 5.0 ± 5.4 m (Mean ± SD, n = 22), the middle carriers a distance of 5.3 ± 6 m (n = 17), and the last carriers one of 16.6 ± 8 m (n = 22). Thus, fragments were mainly transported by the last carriers.

The formation of transport chains: effects of load and body size

We compared the relationship between fragment size and body mass of carriers in a transport chain with that of single carriers, to investigate whether the probability of formation of a transport chain depends on size-matching between workers and loads. Within transport chains, body mass did not differ among first, middle or last carriers. In addition, there was no difference in size between workers in a transport chain, irrespective of their position, and single carriers (Kruskal-Wallis-Test: $H_{(3,75)} = 0.44$, $p = 0.9$). Regarding fragment size, neither fragment mass nor fragment length differed significantly between fragments transported by chains and those transported by single carriers all the way (fragment mass: U = 130, n = 16/22, p = 0.2, NS; fragment length: U = 119.5, p = 0.09, NS).

Regarding size-matching in a transport chain, there was only a significant positive relationship between fragment mass (but not fragment length) and body mass of the *last carriers*, i.e., those that covered the longest distance (Fragment mass: $y = 1.1 + 0.9x$, $r^2 = 0.39$, $p < 0.05$; Fragment length: $y = 14.6 + 1x$, $r^2 = 0.15$, $p = 0.2$, NS). In contrast, no relationships were found for *first carriers* (Fragment mass: $y = 10.7 - 0.2x$, $r^2 = 0.02$, $p = 0.9$, NS; Fragment length: $y = 21.5 + 0.2x$, $r^2 = 0.008$, $p = 0.6$, NS), or *single carriers* (Fragment mass: $y = 6.7 - 0.006x$, $r^2 = 0.00003$, $p = 0.2$, NS; Fragment length: $y = 22.4 - 0.4x$, $r^2 = 0.02$, n = 16, $p = 0.4$, NS).

Transport chains when harvesting natural plants

When harvesting natural fragments out of *Cyperus* plant at 10 m from the nest (n = 37), most cutters dropped them after cutting (42%) or laid them down after less than 1 meter of transport (27%), i.e., shortly after reaching the main trail. Considering all fragments that arrived at the nest, cutters carried directly only 17% of them, single carriers 47%, and the remaining 36% was transported by a chain (Fig. 5). When compared with paper fragments, plant fragments were transported slightly more often by chains (Chi-Square-Test: $\chi^2 = 4.00$, $p = 0.05$). On the 10 m trail, the median "waiting time" of natural fragments was 2 min 9 s (n = 29), being similar to that of paper fragments 2 min 30 s (U = 492, Z = –0.4, p = 0.7, NS). Taken together, these measurements indicate that paper fragments were not dropped as an experimental artefact.

Discussion

Cutting behavior and fragment dropping on the trail

Workers of the grass-cutting ant *Atta vollenweideri* use multi-stage foraging strategies with elaborate task partitioning. On long trails, more than half of the fragments were transported by chains, i.e., beside the cutter mostly two or three carriers transported the load sequentially. Cutting and carrying of fragments were clearly separated activities fulfilled by distinct worker groups differing in body size. Since leaf cutting is an energetically extremely intense activity (Roces and Lighton, 1995), much more demanding than load carriage (Lighton et al., 1987), colonies seem to allocate large workers to the most energy-demanding activity, as intuitively expected.

The proportion of cutters carrying their fragments directly to the nest largely depended on distance, while the probability of dropping a fragment immediately after cutting did not differ between the 10 and the 28 m trail. This indicates that the behavior of cutters was invariant once at the cutting site. On the trail, cutters did not drop their fragments at particular locations, and considering that the covered distance did not correlate with either ant or fragment size, cutters seem to differ in their threshold for dropping. These observations add to other leaf-cutting ant responses that depend on trail distance, as fragment-size determination (*Acromyrmex lundi*, Roces, 1990a; *Atta vollenweideri*, Röschard and Roces, 2003; but not observed in *Atta cephalotes* and *A. colombica*; Wetterer, 1991; Shutler and Mullie, 1991), the extent of size-matching between body and fragment size (Röschard and Roces, 2003), and the distribution of foragers of different size along the trail (Shutler and Mullie, 1991).

What variables motivate workers to drop their fragments, thus leading to the formation of transport chains? First, ants might decide to drop fragments that are not sufficiently attractive, thus rejecting them. But as nearly all dropped fragments were retrieved again, this appears to be very unlikely. Dropping might have occurred because a mismatch between body 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, 2002). Yet, first carriers and single carriers did not differ in size, and their fragments were also similar. 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 via transport chains leads to a better size-matching between worker and load, a phenomenon similar to that recently reported for the same species (Röschard and Roces, 2003), for the seed-harvesting ant *Messor barbarus* (Reyes-López and Fernández-Haeger, 2001), but not for *Atta colombica* workers retrieving cached leaf fragments (Hart and Ratnieks, 2001a).

Transport chains: maximization of leaf delivery rate?

What are the advantages of fragment dropping and the subsequent formation of transport chains? Since all dropped fragments on the trail are afterwards retrieved by nestmates, fragment dropping may allow cutters to quickly return to the selected plant for further harvesting. While this argument accounts for the dropping behaviour of *cutters*, the question arises why *carriers* drop the fragments once more and walk back towards the source, thus being restricted to a shorter section of the trail (compared to a non-partitioned transport modality).

In a recent theoretical account, Anderson et al. (2002) discussed several advantages and disadvantages of co-operative transport modalities that exclusively use *direct* transfer between individual workers and have no predetermined transfer locations. Such "bucket brigades" (*sensu* Anderson et al., 2002), in which all fragments and workers are always on the move, may enhance the performance efficiency of individuals, so that workers are more likely to become specialists and thus more efficient. In addition, true bucket brigades may reduce queuing delays at the source and destination, so that the group's overall rate of resource transportation would be higher.

In *A. vollenweideri*, however, only 12.5% of grass fragments are transferred directly, i.e., most fragments are dropped on the trail and delays occur. Regarding the possible adaptive value of transport chains in *A. vollenweideri*, a tempting hypothesis refers to the efficiency of load transport. Sequential transport *via* a transport chain might be faster than transport by single carriers, thus enhancing colony-wide material intake rates. For the sake of simplicity, we would like to term these arguments as the "economic-transport hypothesis". It should be noted that "economic" in this context refers to the maximization of the transportation speed of a leaf fragment (Lutz, 1929; Rudolph and Loudon, 1986), which at the colony level may result in an increased overall rate of resource transportation. Maximization of leaf transportation has been proposed as a foraging criterion for workers of three leaf-cutting ant species that transfer loads or cache fragments on the ground (Fowler and Robinson, 1979; Hubbell et al., 1980; Anderson and Jadin, 2001). Direct leaf transfer between *Atta colombica* workers, which occurs only in 9% of the transported fragments, resulted indeed in a higher transportation speed after transfer, although transferred fragments did not travel faster than those not transferred (Anderson and Jadin, 2001). In another study on the same species, however, fragments recovered from a cache were transported back to the nest more slowly than normally foraged leaf fragments (Hart and Ratnieks, 2001a), so that the adaptive value of such response remains obscure.

In the present study, transport time of fragments carried by a chain was 25% longer, in average 8 min longer, 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 the dropped fragments, and the handling time by the subsequent foragers. Differences in travel speed between carriers in a transport chain and single carriers are unlikely, as there were no differences in body size. Thus, in terms of foraging time and material transport rates, sequential transport by chains was less efficient than transport by single carriers.

Transport chains: improved information transfer?

A possible adaptive value of transport chains may be related to an improved information transfer. We suggest the following scenario: The sequential transport of fragments leads to an increase in the information flow along the foraging trail, in such a way that more workers, either via direct transfers or upon finding a dropped fragment, get informed about the kind of resource being actually harvested. An improved information transfer may result, because of new recruitment, in an increased overall rate of resource transportation. Based on this "information-transfer hypothesis", the behavioral response of transferring fragments, either directly or indirectly, 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 at the level of the individual fragment. This information-transfer hypothesis is based on arguments previously advanced for honeybees and leaf-cutting ants (Núñez, 1982; Roces, 1993; 2002; Roces and Núñez, 1993).

Whether transport chains indeed accelerate the transfer of information regarding the plant species being actually harvested remains at present elusive, but it is important to consider 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 after a given distance may allow cutting workers to quickly go back to the harvesting plant, making it easier for them to find again the source following the freshly-deposited pheromone trail (Fowler and Robinson, 1979; Hubbell et al., 1980). More important, moving along a short trail sector during foraging may enable workers to reinforce the pheromonal marking much stronger than if they walk all the way to the nest. Hence, recruitment might be reinforced, leading to a quicker monopolisation of the plant being harvested, as demonstrated for first carriers of the leaf-cutting ant *Atta sexdens* (Fowler and Robinson, 1979; Hubbell et al., 1980). We usually observed first carriers turning back and returning to the patch after dropping their fragments (unpublished results; see also López et al., 2000).

Second, 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 transporting on the trail (Roces, 1990b; Roces, 1994; Howard et al., 1996). 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, even those that continued their way to the patch without load. Thus, outgoing foragers may obtain information about the resources being actually harvested both by contacting laden nestmates along the trail, and upon finding a dropped fragment on the trail during its "waiting time". This information may lead outgoing workers to search for a particular plant species, thus redirecting workers from the trail to the new plant.

Information transfer for a 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 at a given patch composed by grasses of different species. 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 that makes it unpalatable, or differences in plant quality, may play a role (Vicari and Bazely, 1993), but there are no studies on this phenomenon. Whatever the reasons, a frequent switch between harvested plants needs a communication system enabling a rapid transfer and update of information.

Up to now, both the information-transfer and the economic-transport hypotheses remain at the descriptive level, as no predictions of one of them have been experimentally addressed. For instance, if transport chains are formed in order to speed up leaf transport, they should be expected to occur when the transporting ants move too slowly, for example when ants carry relatively large fragments. Based on the information-transfer hypothesis, transport chains are expected to occur more frequently under conditions in which information is worth transferring, for instance upon discovery of high-quality resources or when the colony is starved (Roces, 2002; Roces and Hölldobler, 1994). Field experiments aimed to explicitly test predictions derived from these two hypotheses are already under way.

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