

Flavio Roces · Bert Hölldobler

## Leaf density and a trade-off between load-size selection and recruitment behavior in the ant *Atta cephalotes*

Received: 29 July 1993 / Accepted: 2 November 1993

**Abstract** This study considers the interplay between individual load-size selection and recruitment behavior in the leaf-cutting ant *Atta cephalotes*. Foraging workers anchor themselves on the leaf edge by their hind legs and pivot around them while cutting arcs from leaves. Since workers not only cut leaves but also lay chemical trails to recruit nestmates, we investigated whether there is conflict of motivation affecting the workers' decision either to quickly inform nestmates about a newly discovered food source, or instead to cut full-load leaf fragments, which could delay recruitment. Workers were presented with leaves of privet of three different grades of toughness (measured as leaf density = mass/area) as sources of different quality, and load-size selection and recruitment behavior by harvesting-satiated and harvesting-deprived workers were measured. The following results were obtained. (1) Leaf density affected individual load-size selection: both harvesting-satiated and harvesting-deprived workers were found to cut smaller leaf fragments from the denser leaves. (2) Harvesting-deprived workers cut smaller fragments than harvesting-satiated workers, and therefore saved cutting time. The fragments cut were smaller only during the initial phases of the recruitment process, when information about the discovery needed to be transferred. (3) Harvesting-deprived workers showed higher recruitment rates than harvesting-satiated workers. A considerable number of ants were observed to return to the nest unladen. During the initial phases, the ratio of laden/unladen workers was lower than that for harvesting-satiated workers, and increased with the development of the foraging process. (4) Scout workers confronted with familiar leaves ran back to the nest laying chemical trails without even contacting the leaves. They relied on olfactory cues to start recruiting nestmates, and leaf density played no role in their decisions. (5) When confronted

with unfamiliar leaves, on the other hand, they assessed leaf quality by probing bites at the leaf edge, although no actual cuts occurred. In this situation, the resulting recruitment rates depended on physical leaf traits, being higher for the tenderer leaves. (6) Workers foraging on unfamiliar leaves cut smaller fragments than workers cutting familiar leaves, and most of them displayed trail-laying behavior when returning to the nest. The results support the hypothesis of a trade-off between time spent collecting and that invested to recruit nestmates. During the initial phases of exploitation of a newly discovered food source, workers reduced their individual carrying performance in order to return earlier to the colony for further recruitment.

**Key words** Formicidae · Leaf-cutting ants  
Leaf density · Load-size selection · Recruitment

### Introduction

Foraging by workers of social insect colonies is a complex process in which individual and social aspects interact to determine food intake for the colony as a whole, and ultimately colony reproductive output. In species that forage socially recruitment communication enables a colony to allocate foragers to the exploitation of newly discovered food sources. The temporal development of the recruitment process might therefore be of fundamental importance, since in a competitive environment, colonies should try to monopolize the discovered resources as quickly as possible (Hölldobler 1976; Hölldobler and Wilson 1990).

Food gathering uses both time and energy, and a typical foraging cycle by a member of a social insect colony includes not only the collection and transport of the gathered load, but also the transmission of information about the discovered food source. Thus, one could *a priori* expect a trade-off between time spent collecting and time spent recruiting, if colony foraging performance is enhanced through recruitment communication, even at the expense of reduced individual foraging

F. Roces (✉) · B. Hölldobler  
Theodor-Boveri-Institut, Lehrstuhl für Verhaltensphysiologie  
und Soziobiologie der Universität, Am Hubland,  
D-97074 Würzburg, Germany

performance. Leaf-cutting ants (genera *Atta* and *Acromyrmex*) should be well suited to analyze this interplay between individual and social aspects of foraging, because individuals can, via their cutting behavior, individually determine the fragment size to be cut. In addition, a number of studies have addressed the effects of leaf traits on diet selection by leaf-cutting ants (e.g. Cherrett 1968; Waller 1982; Howard 1988), so that a considerable amount of data are available for comparative analysis.

It has been observed that polymorphic leaf-cutting ant foragers frequently harvest leaf pieces that correspond in mass to that of the ants (e.g., Lutz 1929; Cherrett 1972a). This, in part, results from the geometric method of leaf cutting. Since workers anchor themselves on the leaf edge by their hind legs and pivot around them while cutting arcs out of the leaves, the load-size selected may be directly determined by a fixed reach while cutting, dependent on worker body size (Weber 1972). However, there is evidence that not all ants cut fragments as large as they are able to, which suggests a more dynamic mode of load-size selection in leaf-cutting ants. For instance, foraging distance was shown to affect load-size selection in *Acromyrmex lundii* in such a way that ants cut larger fragments farther from the nest (Roces 1990a). In *Atta cephalotes*, Cherrett (1972a) and Rudolph and Loudon (1986) found that for an ant of a given size there was a negative correlation between leaf density (mass/area) and fragment area cut. However, no effect of either distance or leaf density on load-size selection was found in the same species by Wetterer (1990, 1991), who claimed therefore to find support for the hypothesis of a fixed reach while cutting, a view previously advanced by Lutz (1929) and Weber (1972). The situation is even more complex because *Acromyrmex lundii* workers recruited to a high-quality food source cut smaller fragments than those recruited to a low-quality source, but showed increased recruitment activity (Roces and Núñez 1993). These results, unexpected from the point of view of individual ants, suggest that workers "sacrifice" their individual carrying performance in order to return earlier to the colony for further recruitment, which could result in higher overall gains for the colony.

In this study, we analyzed how physical leaf traits affect foraging behavior at both individual and colony level in the leaf-cutting ant *Atta cephalotes*. We presented ants with leaves of three different grades of toughness (measured as leaf density = mass/area) as sources of different quality, and measured individual load-size selection and recruitment rates. We investigated whether the decision to transfer information about a newly discovered food source would motivate a worker to return to the nest sooner in order to recruit nestmates, which could negatively affect the load-size selection of the worker. This possible trade-off between the two behaviors was investigated by comparing the responses of harvesting-satiated and harvesting-deprived workers to standardized leaves, and the responses of workers to unfamiliar and familiar leaves.

## Material and methods

The study was carried out on a laboratory colony of *Atta cephalotes* collected near La Selva, Guanacaste Province, Costa Rica. At the time of the experiments, the colony was c. 3 years old, and its fungus garden occupied c. 9 l. During the experimental period the colony was primarily fed with leaves of privet (*Ligustrum vulgare*), and the assays were performed with workers cutting leaves in a foraging arena 1 m from the nest.

### Effects of leaf density on load-size selection

In independent assays, workers from a harvesting-satiated colony were presented with leaves of privet (*Ligustrum vulgare*) of three different grades of toughness (leaf density  $D = \text{mass/area}$ ):  $D = 0.22 \pm 0.01 \text{ mg/mm}^2$ ,  $D = 0.33 \pm 0.01 \text{ mg/mm}^2$ , and  $D = 0.40 \pm 0.01 \text{ mg/mm}^2$  (mean  $\pm$  SD; henceforth only mean leaf density will be indicated, which varied by only about 5% in the different experimental series). Leaf density was calculated from the weight of leaf discs of known area, punched from the margins of fresh privet leaves, where the ant cuts normally occur. Individual leaves were pinned to the floor, so that workers had to cut a fragment and could not carry away the whole leaf. Although securely pinned, only the tip of each leaf was in contact with the floor, so that workers had to anchor on the leaf edge while cutting fragments, i.e., they displayed their natural cutting behavior. After cutting leaf fragments, workers were individually collected and both body and load weight were determined to the nearest 0.1 mg. Since leaf-cutting ants often pick up loads dropped by others or take loads from other ants (Fowler and Robinson 1979; Hubbell et al. 1980), workers were immediately collected as they completed their cut, to ensure that the fragments had been cut by the workers under examination. All ants cut regular, approximately semicircular, fragments; no ant was observed cutting at the margins left from previous cuts. For each test series we collected two samples of eight to ten laden workers each: the first sample was taken within the first 15 min of the experiment, and the second one was also collected within 15 min, starting 30 min after the beginning of the assay. This enabled us to analyze possible temporal changes in the workers' cutting behavior. The area of the fragments gathered by the ants was calculated from the weight of the fragments and the leaf density previously measured in standardized leaf discs, as follows: fragment area = fragment mass/leaf density. Fragment area was then regressed on ant weight for different leaf densities, and slopes and elevations of the regression equations were compared by two-tailed *t*-tests (Zar 1984).

We also compared load-size selection among workers that had abundant leaves available with those that were "harvesting-deprived". Since nutrients are ingested by foragers directly from leaves when these are palatable, or from the juice of the fungal staphylae (Littledyke and Cherrett 1976; Quinlan and Cherrett 1979), we applied the term "harvesting-satiated workers" when the colony received abundant leaves once a day, and the assays were performed 12–15 h after foraging. "Harvesting-deprived" workers belong to the same colony, but the assays were performed about 48–72 h after foraging.

Cutting speed was also measured in a number of workers of different size, in order to evaluate the relationship between speed and ant mass for privet leaves of different densities, and to estimate total time spent cutting a whole fragment.

### Effects of leaf density on recruitment rates

For measurements of recruitment rates, workers were presented simultaneously with two patches of leaves (*L. vulgare*) of different density:  $D = 0.22 \pm 0.01 \text{ mg/mm}^2$  and  $D = 0.38 \pm 0.02 \text{ mg/mm}^2$ . Each patch consisted of 30 leaves pinned to the floor as previously described, and each was presented in a separate foraging arena.

Workers leaving the nest gained access to both foraging arenas through an Y-shaped carton bridge. Two days before the assays, we allowed the ants to thoroughly explore the bridge and the arena. Pilot tests had shown that in this way we could control for exploratory recruitments during the food recruitment experiments. In each assay, both patches were simultaneously presented. Scout workers that found the leaves did not cut fragments but began to lay chemical trails on their way to the nest, and two independent recruitment processes simultaneously developed. This procedure was undertaken to control for differences in colony conditions (e.g., number of potential recruits in the nest, nutritional condition) that could affect the results. We counted the number of ants running to and from the nest in intervals of 1 min, alternating the counts between the two branches of the bridge, with a pause of 1 min after two consecutive counts. Each assay lasted c. 30 min because the leaves were almost completely harvested in this period. The number of ants running on the bridge per unit time roughly stabilized after 15–20 min, and showed little variation thereafter. For this phase of the foraging process, the count in which we recorded the highest number of ants running over the branch was chosen and used for further comparisons.

Next we investigated possible cues used by scout ants to evaluate the physical features of the encountered food source. As the first scout workers were observed to run back laying chemical trails without cutting any fragments, we videotaped the initial phases of food discovery and counted the number of initial brief bites at the leaf edge performed by the first five scouts before they ran back. These bites did not produce a cut on the leaf, but only a slight scratch, which could be recognized under the microscope.

Additional details concerning experimental procedures will be given with the results.

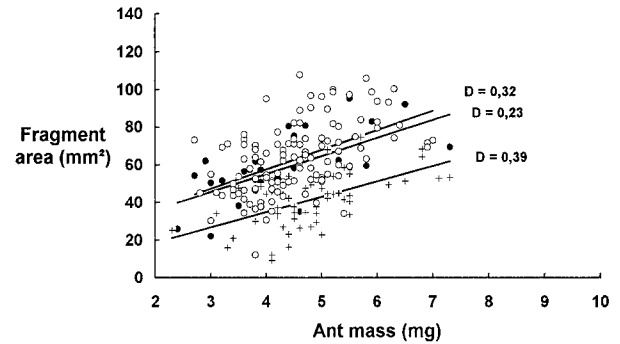
## Results

### Load-size selection

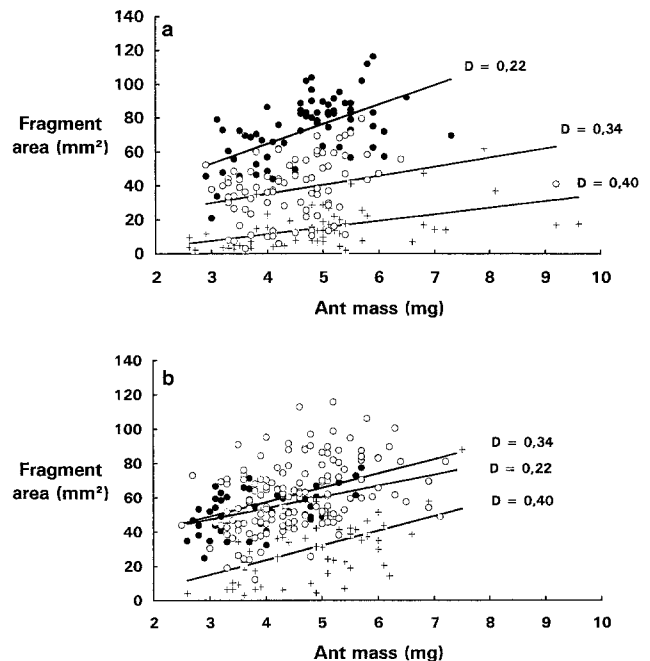
Leaf density affected individual load-size selection by workers of *A. cephalotes*. Harvesting-satiated workers cut smaller fragments from the more denser leaves ( $D=0.39$  mg/mm<sup>2</sup>) than from the tender leaves ( $D=0.23$  and  $D=0.32$  mg/mm<sup>2</sup>) (Fig. 1, data collected in the first 15 min). The slopes of the three curves do not differ statistically ( $D=0.23$  vs  $D=0.32$  mg/mm<sup>2</sup>,  $t=1.09$ ,  $n=152$ ,  $P>0.2$ , NS;  $D=0.23$  vs  $D=0.39$  mg/mm<sup>2</sup>,  $t=1.43$ ,  $n=90$ ,  $P>0.1$ , NS;  $D=0.32$  vs  $D=0.39$  mg/mm<sup>2</sup>,  $t=1.58$ ,  $n=180$ ,  $P>0.1$ , NS), but the ordinate for  $D=0.39$  is statistically different from the others ( $D=0.39$  vs  $D=0.23$  mg/mm<sup>2</sup>,  $t=3.16$ ,  $n=90$ ,  $P<0.005$ ). Roughly similar curves were obtained in the sample of workers collected 30 min after the beginning of the foraging process (data not shown).

A similar relation between load-size selection and leaf density was observed in harvesting-deprived workers. In this case, however, we also found a difference between the sizes selected from leaves of densities  $D=0.22$  and  $D=0.34$  mg/mm<sup>2</sup> (Fig. 2a, data collected within the first 15 min of the foraging process). The elevations of the three curves were statistically different ( $D=0.22$  vs  $D=0.34$ ,  $t=2.89$ ,  $n=150$ ,  $P<0.01$ ;  $D=0.34$  vs  $D=0.40$ ,  $t=3.12$ ,  $n=140$ ,  $P<0.005$ ).

In addition, harvesting-deprived workers generally cut significantly smaller leaf fragments than harvesting-satiated workers, for both leaf densities  $D=0.34$  and

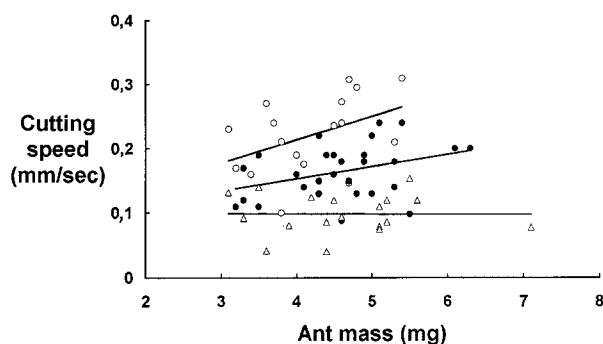


**Fig. 1** Linear regressions of ant mass on fragment area, for harvesting-satiated workers cutting leaves of privet of three different densities. Data collected within the initial 15 min of the foraging process. Least-square fit for  $D=0.23$  mg/mm<sup>2</sup> (full circles):  $Y=9.57X+16.93$  ( $r^2=0.42$ ;  $n=31$ ;  $P<0.001$ ); for  $D=0.32$  mg/mm<sup>2</sup> (open circles):  $Y=10.35X+16.29$  ( $r^2=0.25$ ;  $n=121$ ;  $P<0.001$ ); for  $D=0.39$  mg/mm<sup>2</sup> (crosses):  $Y=8.18X+2.18$  ( $r^2=0.31$ ;  $n=59$ ;  $P<0.001$ )



**Fig. 2** Relationships as in Fig. 1, but workers were harvesting-deprived. Symbols as in Fig. 1. **a** Sample of workers collected during the first 15 min of the recruitment process. Least-square fit for  $D=0.22$  mg/mm<sup>2</sup>:  $Y=11.55X+18.52$  ( $r^2=0.32$ ;  $n=70$ ;  $P<0.001$ ); for  $D=0.34$  mg/mm<sup>2</sup>:  $Y=5.35X+13.81$  ( $r^2=0.09$ ;  $n=80$ ;  $P<0.01$ ); for  $D=0.40$  mg/mm<sup>2</sup>:  $Y=3.90X-4.05$  ( $r^2=0.24$ ;  $n=60$ ;  $P<0.001$ ). **b** Sample collected within 15 min, 30 min after the beginning of the recruitment process. Least-square fit for  $D=0.22$  mg/mm<sup>2</sup>:  $Y=6.54X+27.66$  ( $r^2=0.23$ ;  $n=46$ ;  $P<0.001$ ); for  $D=0.34$  mg/mm<sup>2</sup>:  $Y=8.34X+23.98$  ( $r^2=0.15$ ;  $n=142$ ;  $P<0.001$ ); for  $D=0.40$  mg/mm<sup>2</sup>:  $Y=8.52X-10.51$  ( $r^2=0.26$ ;  $n=59$ ;  $P<0.001$ )

$D=0.40$  mg/mm<sup>2</sup>. The ordinates of the curves for  $D=0.22$  mg/mm<sup>2</sup> do not differ statistically between harvesting-satiated and harvesting-deprived workers ( $t=1.31$ ,  $n=101$ ,  $P>0.1$ , NS), but a significant difference was found for  $D=0.34$  mg/mm<sup>2</sup> ( $t=3.35$ ,  $n=201$ ,



**Fig. 3** Linear relationships between cutting speed and ant mass, for workers harvesting privet leaves of three different densities. Least-square fit for  $D=0.22$  mg/mm<sup>2</sup> (open circles):  $Y=0.036X+0.069$  ( $r^2=0.20$ ;  $n=18$ ;  $P<0.07$ ); for  $D=0.34$  mg/mm<sup>2</sup> (closed circles):  $Y=0.019X+0.078$  ( $r^2=0.13$ ;  $n=28$ ;  $P<0.06$ ); for  $D=0.40$  mg/mm<sup>2</sup> (triangles):  $Y=-0.00047X+0.101$  ( $r^2=0.002$ ;  $n=17$ ;  $P>0.2$ )

$P<0.001$ ) and  $D=0.40$  mg/mm<sup>2</sup> ( $t=3.19$ ,  $n=119$ ,  $P<0.002$ ).

In contrast to harvesting-satiated workers, harvesting-deprived workers modified their load-size selection as the foraging process progressed (Fig. 2b). For both leaf densities,  $D=0.34$  and  $D=0.40$  mg/mm<sup>2</sup>, workers of the sample collected 30 min after the beginning of the assay cut larger fragments than those cut in the initial 15 min. The comparisons between ordinates of the curves of Figs. 2a and 2b show a slight statistic difference for  $D=0.22$  mg/mm<sup>2</sup> ( $t=1.98$ ,  $n=116$ ,  $P<0.05$ ), and a high difference for  $D=0.34$  mg/mm<sup>2</sup> ( $t=3.32$ ,  $n=222$ ,  $P<0.001$ ) and  $D=0.40$  mg/mm<sup>2</sup> ( $t=3.18$ ,  $n=119$ ,  $P<0.002$ ). Note that the load-size selection observed in harvesting-deprived workers 30 min after the beginning of the assay (Fig. 2b) roughly resembles that observed in harvesting-satiated workers (Fig. 1).

The relationship between cutting speed and ant mass for privet leaves of different densities is shown in Fig. 3. As expected, workers foraging on tender leaves cut faster than those on tougher leaves. Using the measured cutting speeds and the data on load-size selection presented above, total time spent cutting a fragment by

both harvesting-satiated and harvesting-deprived workers could be readily estimated. With the assumption that the fragments were semicircular in shape, we first calculated the radius of the fragments from data of fragment area, and from that we obtained the total length cut. Subsequently, total time spent cutting by individual workers could be easily derived by dividing the length cut (mm) by the cutting speed (mm/s).

Total time spent cutting a whole leaf fragment is presented in Table 1, for leaves of three different densities. Harvesting-satiated workers spent more time cutting fragments from leaves with higher density, both in the first (approximately 15 min) and late phases of the recruitment process. This pattern was also observed in harvesting-deprived workers, but only in the advanced phase of the recruitment process. In the first phase, we found a remarkable difference: the ants gained time by cutting smaller fragments, but only when foraging on dense leaves. Time saving varied from 27 to 64 s. As a result, total time spent cutting during the initial phase was roughly similar for all kinds of leaves.

#### Recruitment rates

Leaf density had no effect on the number of harvesting-satiated workers recruited to familiar privet leaves (Table 2). It was observed that the scout ants approached the leaves and ran back to the nest laying trails without even contacting the leaves. The number of probing bites at the leaf edge performed by these first scout workers was low, averaging 0.6–0.8 bites per worker irrespective of leaf density (Table 2). Since in this experiment the leaves were familiar to the ants, it seems conceivable that they were recognized by their odor, which elicited recruitment irrespective of their physical features. To explore the effect of familiarity of the food source on recruitment activity in harvesting-satiated workers, we presented leaves of privet that were impregnated with an unfamiliar odor (orange scent). In this case, the number of bites by scouts at the leaf edge was significantly higher than in tests with familiar leaves; there was no difference between tender and

**Table 1** Total time spent cutting a whole leaf fragment (mean  $\pm$  SD) from privet leaves of different densities, by both harvesting-satiated and harvesting-deprived workers. Data pooled irrespective of worker polymorphism, and compared by two-way ANOVA. Values sharing the same letter are not statistically different ( $P<0.01$ )

Mean leaf density (mg/mm <sup>2</sup> ):	Time spent cutting a fragment (s) from leaves of the following densities:		
	$D=0.22$	$D=0.34$	$D=0.40$
<b>HARVESTING-SATIATED WORKERS</b>			
First 15 min of the recruitment process	86.6 $\pm$ 12.7 <sup>a</sup> ( $n=31$ )	116.5 $\pm$ 15.8 <sup>b</sup> ( $n=121$ )	148.2 $\pm$ 27.3 <sup>c</sup> ( $n=59$ )
<b>HARVESTING-DEPRIVED WORKERS</b>			
First 15 min of the recruitment process	91.0 $\pm$ 12.3 <sup>a</sup> ( $n=56$ )	93.3 $\pm$ 24.5 <sup>a</sup> ( $n=79$ )	84.4 $\pm$ 32.2 <sup>a</sup> ( $n=56$ )
30 min after the beginning of recruitment	87.6 $\pm$ 12.5 <sup>a</sup> ( $n=46$ )	120.6 $\pm$ 19.4 <sup>b</sup> ( $n=142$ )	127.7 $\pm$ 41.2 <sup>b</sup> ( $n=59$ )

**Table 2** Maximum number of ants counted during one 1-min interval, which were recruited to both tender and tough *Ligustrum vulgare* leaves (mean leaf density expressed in mg/mm<sup>2</sup>). Data collected both under harvesting-satiated and harvesting-deprived conditions. The number of probing bites at the leaf edge

(mean  $\pm$  SD) performed by the first scout workers before they returned to the nest is also presented. Data compared by two-way ANOVA. Values sharing the same letter are not statistically different ( $P < 0.01$ )

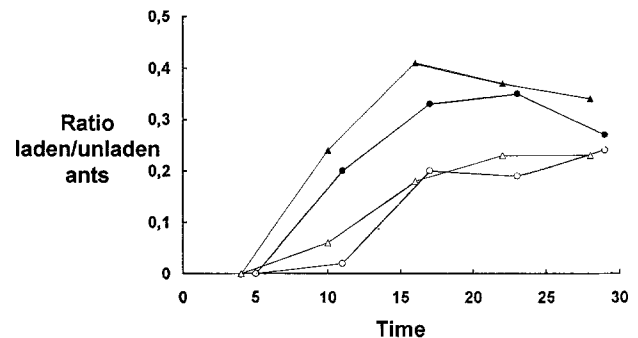
Leaves offered	Maximum number of outbound workers/min		Number of bites at the leaf edge/first 5 scout workers	
	Tender leaves ( $D=0.22$ )	Dense leaves ( $D=0.38$ )	Tender leaves ( $D=0.21$ )	Dense leaves ( $D=0.39$ )
<b>HARVESTING-SATIATED WORKERS</b>				
<i>Ligustrum</i> leaves	41.2 $\pm$ 16.2 <sup>a</sup> ( $n=5$ )	40.2 $\pm$ 12.2 <sup>a</sup> ( $n=5$ )	3.2 $\pm$ 1.3 <sup>d</sup> ( $n=5$ )	3.6 $\pm$ 1.7 <sup>d</sup> ( $n=5$ )
Odor-impregnated leaves (unfamiliar odor)	39.0 $\pm$ 11.9 <sup>a</sup> ( $n=5$ )	16.6 $\pm$ 6.8 <sup>b</sup> ( $n=5$ )	10.4 $\pm$ 2.1 <sup>c</sup> ( $n=5$ )	11.4 $\pm$ 1.8 <sup>c</sup> ( $n=5$ )
Odor-impregnated leaves (familiar odor)	33.0 $\pm$ 7.7 <sup>a</sup> ( $n=5$ )	35.8 $\pm$ 14.0 <sup>a</sup> ( $n=5$ )	4.0 $\pm$ 1.6 <sup>d</sup> ( $n=5$ )	4.6 $\pm$ 1.7 <sup>d</sup> ( $n=5$ )
<b>HARVESTING-DEPRIVED WORKERS</b>				
<i>Ligustrum</i> leaves	47.0 $\pm$ 13.5 <sup>c</sup> ( $n=5$ )	50.4 $\pm$ 16.0 <sup>c</sup> ( $n=5$ )	2.6 $\pm$ 2.1 <sup>d</sup> ( $n=5$ )	2.6 $\pm$ 1.5 <sup>d</sup> ( $n=5$ )
Odor-impregnated leaves (unfamiliar odor)	55.8 $\pm$ 6.5 <sup>c</sup> ( $n=5$ )	54.2 $\pm$ 9.4 <sup>c</sup> ( $n=5$ )	4.8 $\pm$ 1.8 <sup>d</sup> ( $n=5$ )	5.0 $\pm$ 2.7 <sup>d</sup> ( $n=5$ )

dense leaves (Table 2). In addition, a significantly higher number of ants was recruited to the tender leaves (Table 2).

The logical next step was to feed the colony regularly with odor-impregnated leaves and, after a period of familiarization, to conduct similar assays. The colony was therefore fed with odor-impregnated leaves for 2 weeks, and the harvesting-satiated workers were then tested for possible variation in their recruitment activities. The results are presented in Table 2. No difference in the number of workers recruited to tough or tender leaves was noticed, and the general recruitment activity was comparable to that observed when unimpregnated, familiar privet leaves were presented.

Harvesting-deprived workers also showed no difference in their recruitment rates to tender and tough leaves, even for leaves unfamiliar to the ants (Table 2). The maximum number of workers recruited, however, was generally higher than that observed in harvesting-satiated workers, both for familiar and unfamiliar leaves (for statistical comparisons see legend of Table 2). Finally, the number of probing bites was relatively low and there was no difference for both familiar and unfamiliar leaves (Table 2).

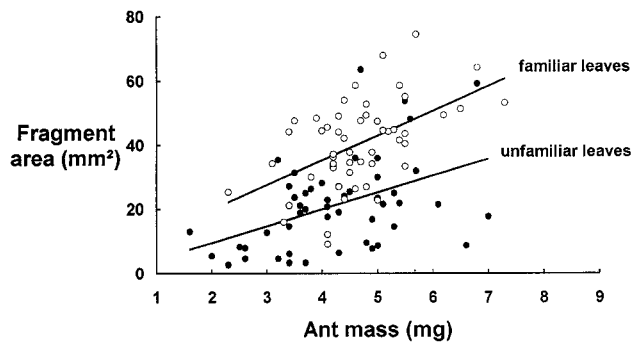
During foraging, a considerable number of ants were observed to return to the nest unladen. The ratio of laden/unladen harvesting-satiated and -deprived workers during foraging is presented in Fig. 4. During the initial phases, this ratio was lower for harvesting-deprived workers. It increased as the foraging process developed, and reached roughly similar values, irrespective of the workers' condition. The ratio was roughly similar for tender and tough leaves.



**Fig. 4** Mean ratio of laden to unladen workers during the recruitment process, both for harvesting-satiated and harvesting-deprived ants. Workers foraged on familiar privet leaves of different densities. The recruitment was started at time = zero. Each figure represents the mean value of five replicates. Full symbols correspond to harvesting-satiated workers, and open symbols to harvesting-deprived workers. Triangles: tender leaves; circles: dense leaves

#### “Novelty” effect of a food source

As reported in the previous section, harvesting-satiated workers foraging on unfamiliar leaves showed more “probing” of the leaves, and in this situation recruitment rates appear to depend on physical leaf traits. Do the foragers also modify their load-size selection when harvesting unfamiliar leaves? It is known that unfamiliar food sources are readily preferred by leaf-cutting ants (Cherrett 1972b). We took advantage of this fact and performed a stricter test of the hypothesis that workers reduce their load-size selection when information about a newly discovered food source is to be transferred. Harvesting-satiated workers were presented with standard-



**Fig. 5** Linear regressions of ant mass on fragment area, for harvesting-satiated workers that cut either familiar or unfamiliar leaves of privet ( $D=0.34 \text{ mg/mm}^2$ ). Data collected within the first 15 min of the experiments. Least-square fit for familiar leaves:  $Y=7.73X+4.41$  ( $r^2=0.27$ ;  $n=52$ ;  $P<0.001$ ); for unfamiliar leaves:  $Y=5.22X-0.82$  ( $r^2=0.20$ ;  $n=50$ ;  $P<0.01$ )

**Table 3** Percentage of laden workers laying chemical trails on their way to the nest, when carrying fragments of either familiar or unfamiliar privet leaves (mean leaf density =  $0.34 \text{ mg/mm}^2$ ; for further details see text). Workers were harvesting-satiated. Data collected within the first 15 min of the recruitment process, in five different experiments. Speed of outbound workers recruited to both kind of leaves is also presented

	Familiar leaves	Unfamiliar leaves	Statistic	<i>P</i>
Percentage of laden workers laying trails	25% ( <i>n</i> = 52)	80% ( <i>n</i> = 50)	$G = 5.49^a$	<0.02
Speed of outbound workers (mm/s)	$30.02 \pm 5.53$ ( <i>n</i> = 52)	$36.13 \pm 5.36$ ( <i>n</i> = 50)	$t = 5.66^b$	<0.001

<sup>a</sup> *G* value from log-likelihood *G*-test, for goodness of fit to the ratio 1:1

<sup>b</sup> *t* value from two-tailed Student's test

ized leaves of privet ( $D=0.34 \text{ mg/mm}^2$ ) and the load sizes selected were compared after the following manipulations: (i) the colony was fed daily on these leaves for 2 weeks, and (ii) the colony was deprived of them for a similar period, but fed daily on different leaves (*Prunus laurocerasus*, Rosaceae). This procedure allowed the "novelty" effect of standardized privet leaves to be analyzed, but avoided harvesting deprivation of the colony.

Harvesting-satiated workers cut smaller fragments from unfamiliar privet leaves than from familiar ones (Fig. 5,  $t=4.75$ ,  $n=102$ ,  $P<0.01$ ), despite the fact that both kinds of leaves presented similar characteristics. In addition, a significantly higher number of workers cutting unfamiliar leaves displayed recruitment behavior (dipping of the gaster tip to the ground, a behavior that indicates trail-pheromone deposition; Moser and Blum 1963) on their way to the nest (Table 3, for comparisons see legend). Outbound (unladen) workers recruited to unfamiliar leaves also ran faster than those recruited to familiar leaves (Table 3).

## Discussion

The hypothesis that workers reduce the load size selected when information about a newly discovered source is to be transferred is supported by the comparison of the behavior of harvesting-deprived and harvesting-satiated workers. Harvesting-deprived workers cut smaller leaf fragments than harvesting-satiated workers, for dense leaves of  $D=0.34$  and  $0.40 \text{ mg/mm}^2$  (Figs. 1 and 2), saved cutting time (Table 1) and showed higher recruitment rates (Table 2). However, food deprivation had no effect on the load sizes selected from the less dense leaves ( $D=0.22 \text{ mg/mm}^2$ ), from which workers cut the largest fragments. The comparison between the load sizes selected during the first 15 min and 30 min after the beginning of recruitment also showed that harvesting-deprived workers cut smaller fragments and saved cutting time only during the initial phases of the recruitment process, when information about the discovery needs to be transferred (Fig. 2a vs Fig. 2b; Table 1). In addition, harvesting-deprived ants had a greater tendency to return to the nest for recruitment without cutting any fragments (Fig. 4). This suggests the existence of two conflicting motivations in this initial phase of exploitation of a new food source: "cut a fragment" or "recruit nestmates". While it is known that a number of incoming unladen ants in the field clear the trail or transport plant sap (Daguerre 1945; Stradling 1978), this consideration could provide one of the possible explanations why a considerable percentage of workers on an active foraging trail in the field return to the nest unladen (13–75%: Hodgson 1955; Cherrett 1972a; Lugo et al. 1973; Lewis et al. 1974).

The importance of information transfer as a factor modulating load-size selection was evident when the "novelty" effect of a food source was analyzed. Unfamiliar food sources are highly attractive and readily preferred by leaf-cutting ants (Cherrett 1972b). In our study, workers foraging on the more attractive unfamiliar leaves cut smaller fragments than those visiting familiar leaves (Fig. 5), and a higher proportion of them engaged in trail-laying on their way to the nest (Table 3). Time saved by cutting smaller fragments, higher recruitment activity and increased running speed due to the smaller loads (Lighton et al. 1987) are expected to promote a rapid increase in the number of ants recruited to the most attractive (unfamiliar) food source, even at the expense of reducing individual load-carrying performance. The speed of outward bound recruited workers also contributed to a rapid amplification and establishment of a recruitment process: they ran faster when recruited to unfamiliar than to familiar leaves (Table 3). These results also showed that, on their first trip to the nest, the speed of recruited ants depended on the intensity of recruitment signals, as recently reported (Roces 1993a).

Interestingly, even though workers (either harvesting-satiated or harvesting-deprived) cut smaller fragments from the denser leaves, there was no difference in

recruitment rates when leaves were familiar to the ants (Table 2, first row). The low frequency of probing bites at the leaf edge by the first scout workers indicates that leaves were primarily recognized by their odor. It is known that foraging leaf-cutting ants orient upwind to leaf-odor stimuli (Littleddyke and Cherrett 1978), and that they use learned odor cues as decision criteria during diet selection (Roces 1990b, 1994). Under our experimental conditions, scout workers always returned to the nest without cutting any leaf fragments, but laying chemical trails. They relied on olfactory cues to start recruiting nestmates, and the temporal development of recruitment was observed to be independent of physical leaf traits. When leaves were impregnated with an unfamiliar odor, on the other hand, the scout ants exhibited an increased biting frequency before they recruited nestmates, and recruitment rates were higher for the more tender leaves (Table 2). It indicates that scouts encountering unfamiliar leaves assess leaf quality by biting the leaves, and the information gathered in this way subsequently affects the recruitment activity. It should be pointed out that no actual cuts occurred when scout workers bit the leaf edge. After a period of familiarization with the novel odor, the workers showed a low biting frequency and the recruitment rates became independent of leaf density. This suggests that olfactory cues from leaves learned by the workers were involved in determining food preference.

Harvesting-deprived workers, on the other hand, showed an increased readiness to forage, and the observed recruitment rates were independent of physical leaf traits. They were higher than those recorded in harvesting-satiated workers (Table 2), as previously reported (Jaffé and Howse 1979). Biting frequency, however, remained low even for leaves unfamiliar to the ants, indicating a reduction in selectivity with increasing foraging motivation.

As mentioned above and observed by Jaffé and Howse (1979), the first scout ants always did not cut fragments from the newly discovered food source, but returned to the nest displaying recruitment behavior. In the leaf-cutting ant species *Acromyrmex lundii*, the information transferred by these successful scouts is of fundamental importance for the establishment of the recruitment process (Roces and Núñez 1993). This decisive role of the information transferred by the first scouts could explain why similar recruitment rates were recorded for familiar leaves of different density. However, it is unknown to what extent the trail-laying activity of the laden ants also contributed to the temporal development of the recruitment process. Assuming that the recruitment rates were mainly determined by the trail-laying activity of the first successful scouts, why did recruited ants show a trade-off between individual load-size selection and recruitment behavior? In addition, if workers selected smaller loads to save time for further recruitment, it would be expected that workers change to select larger loads for all types of leaves when the recruitment has been stabilized, as observed for inter-

mediate leaf densities (Fig. 2). This was not the case for the denser leaves. Workers of *Atta cephalotes* (either harvesting-satiated or harvesting-deprived) continued cutting smaller fragments than those cut from the more tender leaves. More puzzling, workers foraging on unfamiliar leaves also selected smaller loads from the unattractive, denser leaves, but recruitment rates were even lower for these leaves (Table 2). It follows that, under given feeding conditions, the selection of small loads from dense leaves did not contribute to more intense recruitment. It is *a priori* conceivable that workers foraging on the denser leaves could cut larger fragments by simply extending their "reach" while cutting, but they did not. Why do ants not cut larger fragments, if they are capable of doing so? For a leaf density of 0.40 mg/mm<sup>2</sup>, for instance, a worker has to make the same trip almost twice to gather the same load it would gather if it would cut a full-size fragment. As shown in this study, it has been reported several times that cutting speed depends on physical leaf traits, i.e. ants foraging on tougher leaves cut more slowly than on tender leaves (Cherrett 1972a; Wilson 1980; Nichols-Orians and Schultz 1989). Moreover, ants prefer tender leaves due to ease in cutting, even though these leaves are chemically less palatable because of higher concentrations of secondary compounds (Waller 1982; Nichols-Orians and Schultz 1989, 1990). Cutting larger fragments from the denser leaves might result in excessive time and/or energy spent at the food source. This energy expenditure could reduce foraging frequency by increasing the recuperative time of the workers at the nest, and may therefore prevent workers to forage on more attractive sources. But these considerations are only speculations; this issue remains to be further investigated.

It is worth mentioning that a negative correlation between leaf density and fragment area cut by workers of *Atta cephalotes*, as reported here, has previously also been found by Cherrett (1972a) and Rudolph and Loudon (1986), but Wetterer (1991) found that the area cut by an ant of a given size showed no significant difference among leaves of three different densities. He used, however, a low and narrow range of leaf densities (0.21–0.30 mg/mm<sup>2</sup>) compared with that used by us (0.22–0.40 mg/mm<sup>2</sup>) and those measured in previous studies [leaves from c. 0.12 to 0.48 mg/mm<sup>2</sup> in Cherrett (1972a, and personal communication) and of 0.159 and 0.575 mg/mm<sup>2</sup> in Rudolph and Loudon (1986)]. Therefore, lack of evidence in his study [and also in Wetterer (1990), with densities of 0.17 and 0.28 mg/mm<sup>2</sup>], cannot rule out the possibility of flexible leaf-cutting behavior of individual ants foraging on leaves of different densities. It is important to mention that, even though workers in our study had a reduced range of body sizes, our results for the more tender leaves ( $D=0.22$  and  $0.32-0.34$  mg/mm<sup>2</sup>, Figs. 1, 2b) fit well into the relationship between ant mass and fragment area presented by Wetterer (1991) for all types of leaves he used. Interestingly, within this range of leaf densities we also observed reduced load-size selection in harvesting-deprived workers, but only



during the first phases of the recruitment process (for  $D=0.34 \text{ mg/mm}^2$ , cf. Fig. 2a and b). The fact that we obtained a roughly constant load-size selection for the more tender leaves, irrespective of both harvesting-deprivation and time elapsed since the beginning of the recruitment (Figs. 1 and 2), suggests that leaves used by Wetterer (1991), although of different density, fell within the ants' assessment of quality range "tender". The reduced load-sizes cut from the denser leaves in our study ( $D=0.40 \text{ mg/mm}^2$ ) cannot be satisfactorily described by the relationship presented by Wetterer (1991).

The hypothesis of a trade-off between time spent collecting and that invested to recruit nestmates was previously put forward for ants by Rocés and Núñez (1993), and finds further support in the present study when: (i) the behavior of harvesting-deprived and harvesting-satiated workers is compared (Fig. 1 vs Fig. 2; Fig. 4; Tables 1 and 2); (ii) the effects of the different phases of recruitment are considered (Fig. 2a vs Fig. 2b); and (iii), the novelty effect of a source is analyzed (Fig. 5; Table 3). Our results indicate that, in the initial phases of a recruitment process, the tendency of transfer information about a newly discovered food source motivated a worker to shorten the cutting behavior and return to the nest in order to recruit additional nestmates. Its individual performance as collector was therefore reduced but the colony as a whole increased its feeding rate due to the recruited workers which joined in the resource-gathering activity. The unexpected results obtained for workers cutting dense leaves, which do not fit predictions derived from the information-transfer hypothesis, stimulate further research on the proximate determinants of load-size selection, and its contribution to colony-wide foraging performance.

**Acknowledgements** We thank J.A. Núñez for helpful discussions, J. Tautz and two anonymous reviewers for comments on the manuscript. F. Rocés was supported by a grant from DAAD and funds of the Deutsche Forschungsgemeinschaft (Leibniz Award to B. Hölldobler); the project was also funded by the SFB 251, Project 18 of the University of Würzburg.

## References

- Cherrett JM (1968) The foraging behaviour of *Atta cephalotes* L. (Hymenoptera: Formicidae). I. Foraging patterns and plant species attacked in tropical rain forest. *J Anim Ecol* 37:387–403
- Cherrett JM (1972a) Some factors involved in the selection of vegetable substrate by *Atta cephalotes* (L.) (Hymenoptera: Formicidae) in tropical rain forest. *J Anim Ecol* 41:647–660
- Cherrett JM (1972b) Chemical aspects of plant attack by leaf-cutting ants. In: Harboure J (ed) *Phytochemical Ecology*. Academic Press, London, pp 13–24
- Daguere JB (1945) Hormigas del género *Atta* Fabricius de la Argentina. *Rev Soc Arg Entomol* 12:438–460
- Fowler HG, Robinson SW (1979) Foraging by *Atta sexdens* (Formicidae: Attini): seasonal patterns, caste and efficiency. *Ecol Entomol* 4:239–247
- Hodgson LD (1955) An ecological study of the behavior of the leaf cutting ant *Atta cephalotes*. *Ecology* 36:293–304
- Hölldobler B (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav Ecol Sociobiol* 1:3–44
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press, Cambridge, Massachusetts
- Howard JJ (1988) Leafcutting ant diet selection: relative influence of leaf chemistry and physical features. *Ecology* 69:250–260
- Hubbell SP, Johnson LK, Stanislav E, Wilson B, Fowler HG (1980) Foraging by bucket-brigade in leaf-cutter ants. *Biotropica* 12:210–213
- Jaffé K, Howse PE (1979) The mass recruitment system of the leaf-cutting ant, *Atta cephalotes*. *Anim Behav* 27:930–939
- Lewis T, Pollard GV, Dibley GC (1974) Rhythmic foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). *J Anim Ecol* 43:129–141
- Lighton JRB, Bartholomew GA, Feener DH (1987) Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol Zool* 60:524–537
- Littlellyke M, Cherrett JM (1976) Direct ingestion of plant sap from cut leaves by the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) (Formicidae: Attini). *Bull Entomol Res* 66:205–217
- Littlellyke M, Cherrett JM (1978) Olfactory responses of the leaf-cutting ant *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) (Hymenoptera: formicidae) in the laboratory. *Bull Entomol Res* 68:273–282
- Lugo AE, Farnworth EG, Pool D, Jerez P, Kaufman G (1973) The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54:1292–1302
- Lutz FE (1929) Observations on leaf-cutting ants. *Am Mus Novit* 388:1–21
- Moser JC, Blum MS (1963) Trail marking substance of the Texas leaf-cutting ant: source and potency. *Science* 140:1228
- Nichols-Orians CM, Schultz JC (1989) Leaf toughness affects leaf harvesting by the leaf cutter ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae). *Biotropica* 21:80–83
- Nichols-Orians CM, Schultz JC (1990) Interactions among leaf toughness, chemistry, and harvesting by attine ants. *Ecol Entomol* 15:311–320
- Quinlan RJ, Cherrett JM (1979) The role of fungus in the diet of the leaf-cutting ant *Atta cephalotes* (L.). *Ecol Entomol* 4:151–160
- Rocés F (1990a) Leaf-cutting ants cut fragment sizes in relation to the distance from the nest. *Anim Behav* 40:1181–1183
- Rocés F (1990b) Olfactory conditioning during the recruitment process in a leaf-cutting ant. *Oecologia* 83:261–262
- Rocés F (1993a) Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundii*) depend on their motivational state. *Behav Ecol Sociobiol* 33:183–189
- Rocés F (1994) Odour learning and decision-making during food collection in the leaf-cutting ant *Acromyrmex lundii*. *Insectes Soc* (in press)
- Rocés F, Núñez JA (1993) Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim Behav* 45:135–143
- Rudolph SG, Loudon C (1986) Load size selection by foraging leaf-cutter ants. *Ecol Entomol* 11:401–410
- Stradling DJ (1978) The influence of size on foraging in the ant, *Atta cephalotes*, and the effect of some plant defense mechanisms. *J Anim Ecol* 47:173–188
- Waller DA (1982) Leaf-cutting ants and live oak: the role of leaf toughness in seasonal and intraspecific host choice. *Entomol Exp Appl* 32:146–150
- Weber NA (1972) *Gardening ants, the Attines*. American Philosophical Society, Philadelphia
- Wetterer JK (1990) Load-size determination in the leaf-cutting ant, *Atta cephalotes*. *Behav Ecol* 1:95–101
- Wetterer JK (1991) Allometry and the geometry of leaf-cutting in *Atta cephalotes*. *Behav Ecol Sociobiol* 29:347–351
- Wilson EO (1980) Caste and division of labor in leaf-cutting ants. II. The ergonomic optimization of leaf-cutting. *Behav Ecol Sociobiol* 7:157–165
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall, New Jersey