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Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundi*) depend on their motivational state

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Summary. During recruitment, running velocity of both outbound and laden workers of the leaf-cutting ant *Acromyrmex lundi* depended on the information about resource quality they received from the first successful recruiter. In independent assays, single scout ants were allowed to collect sugar solutions of different concentrations and to recruit nestmates. Recruited workers were presented with standardized paper discs rather than the sugar solution given to the original recruiting ant. Outbound recruited workers were observed to run faster the more concentrated the solution found by the recruiter. Speed of disc-laden workers also depended on the concentration of the solution found by the recruiter, i.e. on the information about food quality they received, since they had no actual contact with the sugar solution. Disc-laden workers ran, as intuitively expected, slower than outbound workers. The reduction in speed, however, could not be attributed to the effects of the load itself, because workers collecting discs of the same weight, but with added sugar, ran as rapidly as outbound, unladen workers. Workers collecting standardized sugared discs reinforced the chemical trail on their way to the nest. The percentage of trail-layers was higher when workers were recruited to 10% than to 1% sugar solution, even though they collected the same kind of discs at the source. Their evaluation of resource quality, therefore, depended on their motivational state, which was modulated by the information they received during recruitment. Using previously published data on energetics of locomotion in leaf-cutting ants, travel costs of *A. lundi* workers recruited to sugar solutions of different concentration could be estimated. For workers recruited to the more concentrated solution, both speed and oxygen consumption rate increased by a roughly similar factor. Therefore, although workers ran faster to the high-quality resource, their actual energy investment per trip remained similar to that made by workers recruited to the low-quality resource. It is suggested that the more motivated workers reduced travel time without increasing energy costs during the trip. The adaptive value of these responses seems to be related to a rapid transmission of information about a newly discovered food source.

Key words: Leaf-cutting ants – *Acromyrmex* – Foraging – Motivation

Introduction

The ecological success of social insects is considered to lie in part in the ability of a colony to allocate foragers to the exploitation of newly discovered food sources. Through recruitment behavior, successful foragers inform their nestmates about the existence of a food source and orient them to its location. Signals involved in recruitment, of chemical, vibrational or tactile nature, are often considered as releasers of a given specific response. Besides these kinds of signals, there is evidence that some cues do not evoke a particular response. Instead, they influence the behavior of the recipients by modulating their responsiveness, and thereby changing the probability of performance of other behavioral acts. This type of "modulatory communication" has been reported for ants in a number of cases (Fuchs 1976a, b; Markl and Hölldobler 1978). The first analysis of modulatory communication during recruitment used the seed-harvester ant *Novomessor cockerelli*. In this species, information transferred via stridulation signals proved to act as a "communication amplifier" (Markl and Hölldobler 1978), i.e., the perception of stridulation by foraging workers facilitates the release of a short-range recruitment pheromone, resulting in a faster development of the recruitment process than when no stridulation occurs. Enhancement of recruitment by stridulation acting as a modulatory signal has also been observed in other ant species (Hahn and Maschwitz 1985; Baroni-Urbani

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et al. 1988), where the number of recruited ants was higher when stridulation occurred than when it did not.

Workers of some ant species also transfer information about the quality of the food source encountered, i.e., there is a positive relationship between food quality and intensity of the recruitment signals. Recruitment intensity has been measured either as differences in the individual deposition of trail pheromone by recruiters (Hangartner 1969, 1970) or indirectly as the number of recruited ants responding to the chemical trail (Wilson 1962; Hölldobler 1976; Jaffé and Howse 1979; Breed et al. 1987). Changes in the behavior of individual recruited workers after the perception of these graded signals, however, have rarely been investigated (Beckers et al. 1992), despite the fact that they are responsible for the amplification and establishment of the recruitment process.

In this study I ask whether and to what extent communication about resource quality modulates decision-making in recruited workers of the leaf-cutting ant *Acromyrmex lundi,* in an attempt to integrate individual behavior into colony function. During the experiments, attention was not centered on the successful scout ant that initiated recruitment, but in the behavior of recruited workers that were confronted with standardized stimuli rather than with the original food source. Their responses to these stimuli after they had been informed about food sources of different qualities were compared. Evidence is presented that information received by recruited workers from the recruiting ant modulated their motivational state, leading to differences in both their velocity when they returned laden to the nest and their individual evaluation of a given resource quality.

Methods

Two laboratory colonies of the leaf-cutting ant *Acromyrmex lundi* of approximately 1500 workers, reared from the founding queen, were studied. Assays were performed with workers foraging on a table which was connected to the nest by a 1 m long, 2 cm wide wooden bridge.

Effects of the information about resource quality transferred by a single scout ant on the trail-laying behavior and running velocity of recruited workers were studied in two experimental series, using the following basic experimental procedure. A drop of sucrose solution of a given concentration was presented on a plastic dish at the food table. Once the first scout worker found the solution, it imbibed the liquid and returned to the nest showing trail-laying behavior. Other workers on the foraging table were then removed to avoid more recruitment, and the dish with the sugar solution was replaced with a pile of 20 filter-paper discs as standardized material (diameter: 5 mm; weight: 0.80 ± 0.07 mg, $n = 70$, mean ± SE). Discs were previously impregnated with orange scent to ensure attractiveness (see Roces 1990a). Thus, only the worker that had fed on the sugar solution was allowed to return to the nest, ensuring that recruited ants leaving the nest and following the chemical trail have responded to its recruitment signals alone. Shortly afterwards, the first group of recruited workers arriving at the foraging table found paper discs instead of the solution, picked one disc up and carried it readily to the nest. Since the fragment sizes cut by leaf-cutting ants are variable and depend on several parameters (Cherrett 1972; Roces 1990b; Roces and Núñez 1993), this procedure allowed measurement of the responses of recruited workers independent of their cutting activity and only as a function of the information about resource quality they received during recruitment.

Two experimental series were performed. In different assays of the first series, workers were recruited to a given sugar solution (0.5, 1, 10, 20 or 50% sucrose weight/weight). For each assay, the running velocity of the first group of ants recruited by a single scout was recorded along the bridge as they ran towards the foraging table. Their trail-laying activity was also noted, i.e., their touching of the gaster-tips repeatedly to the ground, a behavior that indicates trail-pheromone deposition (Moser and Blum 1963; Jaffé and Howse 1979). Speed and trail-laying were also recorded once these ants picked up a paper disc at the foraging table and returned to the nest. When these laden workers reached the end of the bridge, they were collected individually and the assay concluded. Workers were then weighed to the nearest 0.01 mg and released at the nest entrance. Since a successful scout normally recruited a group of c. 8–12 workers per assay, their responses could easily be monitored, and no attempt was made to mark either the scout or the individual recruits in order to avoid disturbances. Since the speed of the same ant going to and from the food source was not monitored, mean speed of a group of recruits running to and from the nest was compared. Data for 4–8 different recruits were collected per assay, and a total of 22 assays were performed. Since each assay lasted a few minutes, there was no possibility that a given recruited ant had made more than one trip to the source.

In the second experimental series, effects of load mass on velocity and trail-laying behavior of workers recruited to different sugar solutions were analyzed. Recruitments were induced with sucrose solutions, either 10% or 1%, and recruited workers found, in different assays, the following substrates:

1. Odor-impregnated paper discs previously soaked in 10% sucrose solution and the dried (henceforth: "sweet-discs"). The weight of the discs (0.82 ± 0.1 mg) did not differ from that of the non-sugared discs used in the first experimental series ($t = 1.32$, $df = 118$, NS). A total of eight assays were performed.
2. Heavier sweet-discs, weighing 1.40 ± 0.11 mg ($n = 8$ assays).
3. Even heavier sweet-discs, weighing 2.21 ± 0.10 mg ($n = 6$ assays).

Discs were produced with a standard paper punch and filter paper of different densities, so that they differed in weight but not in area (5 mm diameter), to keep handling difficulties roughly the same. Comparison between assays using non-sugared and sweet-discs of the same weight allows a distinction of workers' responses that depend on the information they obtained during recruitment (which was similar for workers recruited to a given sugar solution), from those that result from their individual evaluation of resource quality. While it is probable that sweet-discs of different weight contained different amounts of sugar, I compared the behavior of workers recruited to different sugar solutions that collected the same kind of discs.

Because there is considerable worker polymorphism in *A. lundi*, I attempted to obtain a comparable value for the load carried per individual adjusted to size. I calculated the burden in the following way: $B = (M_a + M_l)/M_a$, where M_a = ant mass and M_l = load mass (Rissing 1982). All assays were performed in a random sequence, one each day, at a temperature of 23–24° C.

Results

First experimental series

Over both experimental series, body weight of the participant workers ranged from 0.72 to 5.10 mg (mean ± SD: 2.30 ± 0.80 mg, $n = 373$), and there was no relationship between velocity and worker body weight in any assay performed (after regression analysis; highest $r^2 = 0.042$, $P > 0.1$, NS). For this reason, velocity data have been

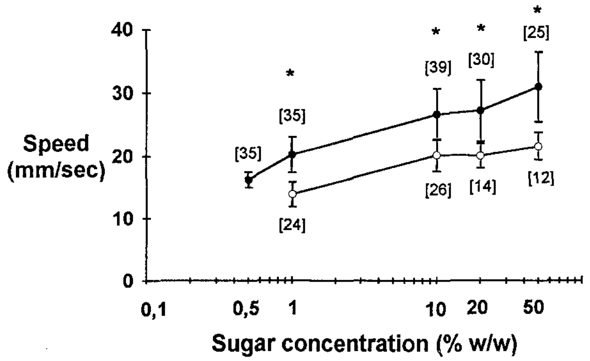

Fig. 1. Speed of ants recruited to different sugar solutions by a single recruiter worker ($\bar{X}\pm$SD). *Closed circles*: outbound, recruited ants. *Open circles*: recruited ants that collected a paper disc and ran laden back to the nest. In *parentheses*: number of observations. Data from the two colonies were pooled (for 0.5% sugar concentration, $n=5$ recruitments; for 1%, $n=5$; for 10%, $n=5$; for 20%, $n=4$; for 50%, $n=3$). *Asterisks:* values for outbound and laden workers are statistically different (two-way ANOVA, $P<0.01$)

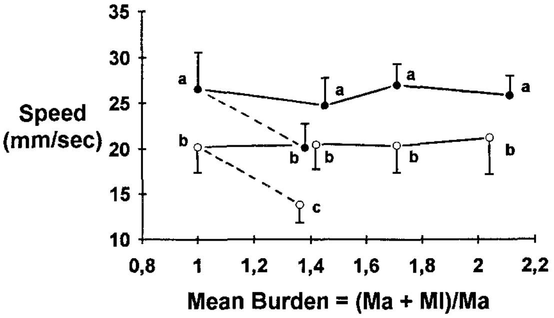

Fig. 2. Speed ($\bar{X}+$SD) of ants recruited either to 10% (*closed circles*) or to 1% sugar solution (*open circles*), as a function of burden, when they carried different kinds of paper discs (sweet-discs: *full line*; standard discs without sugar: *dotted line*). Burden = 1 corresponds to outbound, recruited workers (data from Fig. 1). The increase in burden resulted from an increase in the weight of the collected discs. Values bearing the same *letter* are not statistically different (two-way ANOVA, Scheffe's multiple contrasts, $P<0.01$)

expressed as mean ± SD, irrespective of worker polymorphism. Figure 1 shows the results of the first experimental series. Recruited workers ran faster the higher the concentration of the sugar solution the single recruiter ant previously encountered (Fig. 1, closed circles, linear regression: $y=0.253\,x+20.214$, $r^2=0.45$, $P<0.01$). A similar relationship between speed and sugar concentration was found for laden workers, when they collected and carried non-sugared paper discs back to the nest (Fig. 1, open circles, linear regression: $y=0.135\,x+16.294$, $r^2=0.34$, $P<0.01$).

At each concentration tested, disc-laden workers moved significantly slower than outbound, recruited workers (Fig. 1, comparisons between closed and open circles; two-way ANOVA: $F=177.02$; $df=1{,}197$; $P<0.001$). Surprisingly, workers recruited to 0.5% sugar solution did not collect the non-sugared discs. Although they responded in the nest to the single recruiter ant and arrived at the foraging table, they inspected the discs but were reluctant to collect any one ($n=35$ observations). Throughout this first experimental series, no recruited worker on its way to the food source ($n=164$) nor any incoming one ($n=76$), laden with a disc, was observed laying trails.

Second experimental series

In this series, recruitment was induced with either 10% or 1% sugar solution. I chose these concentrations because of the larger differences in workers' speed recorded in the previous series (see Fig. 1). Trail-laying and speed of workers recruited to these different solutions were compared after they collected standardized sweet-discs, as previously described, instead of sugar solution.

The relationship between velocity and burden for the different assays is depicted in Fig. 2. Speed of both outbound and disc-loaded workers was higher for those recruited to 10% than for those recruited to 1% sugar solution, although the discs collected were of the same kind (comparison between closed and open circles, two-way ANOVA: $F=235.8$; $df=1{,}247$; $P<0.001$). For both concentrations tested, velocity of recruited workers was higher when they carried a sweet-disc than when a non-sugared one of the same weight was transported (for burden = 1.4, comparison between both closed or both open circles, Scheffe's multiple contrasts, $P<0.01$). Since for each kind of disc there was no difference in the relative load carried by ants recruited to 10% or 1% sugar solution (see comparison between columns in Table 1), differences in speed cannot be attributed to an effect of the load itself. In addition, transport of even heavier sweet-discs did not affect velocity at any of the two concentrations tested. Speed of laden workers remained similar to that of outbound workers, even when discs weighed as much as the workers that carried them (Fig. 2, comparisons between disc-laden workers for each concentration, and Table 1).

While in the previous series no reinforcement of the chemical trail was observed when workers carried non-sugared discs, workers carrying sweet-discs displayed trail-laying behavior, but, as expected, only when running back to the nest. For workers carrying standardized sweet-discs, the proportion of trail-layers depended on the concentration of the sugar solution found by the single recruiter ant, even though workers collected the same kind of discs (comparisons between columns, Table 1 on the right). The percentage of trail-reinforcing workers was higher when they were recruited to 10% (c. 75%) than to 1% sugar solution (c. 39%). An increase in the relative weight carried (from burden = 1.4 to 2.1) did not result in any appreciable change in the percentage of recruited workers reinforcing the chemical trail (comparisons along columns, Table 1 on the right).

Estimates of travel costs

Using the equations relating speed and metabolic rate presented by Lighton et al. (1987) for the leaf-cutting

Table 1. Relative load carried (burden) and trail-laying activity of workers recruited to sugar solutions (10% or 1% sucrose w/w) and then collecting standardized paper discs

	Burden ($\bar{X}\pm$SD)		Percentage of trail-laying workers	
Workers recruited:	to 10%	to 1%	to 10%	to 1%
Unladen ants (outbound)	1 ($N=5$; $n=39$)	1 ($N=5$; n$=35$)	0	0
Laden with a paper disc [mean weight (MW) = 0.80 mg]	1.38 ± 0.10^{a} ($N=5$; $n=26$)	1.36 ± 0.11^{a} ($N=5$; $n=24$)	0	0
Laden with a sweet paper disc (MW = 0.82 mg)	1.45 ± 0.09^{a} ($N=4$; $n=27$)	1.42 ± 0.11^{a} ($N=4$; $n=22$)	77.8%^{d}	40.9%^{e}
Laden with a sweet paper disc (MW = 1.40 mg)	1.71 ± 0.12^{b} ($N=4$; $n=24$)	1.71 ± 0.22^{b} ($N=4$; $n=26$)	70.8%^{d}	38.5%^{e}
Laden with a sweet paper disc (MW = 2.21 mg)	2.11 ± 0.24^{c} ($N=3$; $n=18$)	2.04 ± 0.21^{c} ($N=3$; $n=16$)	77.8%^{d}	37.5%^{e}

Data of recruited workers running towards the source are also included

N: number of assays; n: number of observations

Burden values bearing the same letter are not statistically different (two-way ANOVA, Scheffe's multiple contrasts, $P<0.01$)

Figures bearing the same letter are not statistically different (proportions compared by Fischer's exact test; level of significance: $P<0.01$)

ant *Atta colombica*, and the measured speeds of *Acromyrmex lundi*, it is possible to obtain an estimate of the actual costs of travel by this species. In addition, data obtained by *Acromyrmex* allow the travel costs of ants running to food sources of different quality to be compared. This is the first attempt to compare foraging costs in ants with control of the workers' motivational state.

The measured mean speed (±SE) of outbound, unladen *A. lundi* workers recruited to 10% sugar solution was: $V_{10\%}=26.58\pm0.64$ mm/s, while for workers recruited to 1% it was: $V_{1\%}=20.21\pm0.48$ mm/s. Therefore, workers recruited to the richer solution increased their speed by a factor of 1.32 ($V_{10\%}/V_{1\%}$). A similar result arises from calculations for workers laden with sweet-discs, irrespective of load size: an increase in speed by a factor of 1.25 (mean speed: $V_{10\%}=25.82$ mm/s; $V_{1\%}=20.68$ mm/s). Is the parallel increase in the worker's metabolic rate of the same magnitude, thus yielding a constant energy investment per trip independent of travel speed? Lighton et al. (1987) reported a linear relationship between oxygen consumption rate (Y) and running speed (X) for unladen *Atta colombica* workers, as follows:

$$Y=0.72+10.05\,X$$

where Y is ml O_2/g per hour and X is km/h. Using this equation, oxygen consumption for unladen *Acromyrmex lundi* workers recruited to 10% sugar solution results: $Y_{10\%}=1.68$ ml O_2/g per hour, while for those recruited to 1% it is: $Y_{1\%}=1.45$ ml O_2/g per hour. Then, O_2 consumption rate due to the higher speed increased by a factor of 1.16 ($Y_{10\%}/Y_{1\%}$). For ants carrying sweet-discs, it is assumed that travel costs are linearly correlated with speed irrespective of load size, i.e., laden ants do not incur higher travel costs by carrying larger loads. Calculations yielded an increase of the O_2 consumption rate by a factor of 1.13.

In conclusion, speed of ants recruited to 10% was higher than speed of ants recruited to 1%, by a mean factor of 1.29 (unladen + laden workers pooled). Their O_2 consumption rate was also higher, by a mean factor of 1.15. As derived values, these estimates do not have measured errors. Given the standard deviation of the measured speeds in *A. lundi* workers (c. ±13%), it will be assumed that these estimates do not differ significantly.

Discussion

The present results point out the importance of considering the motivational state of foraging workers when their behavior is under scrutiny. This aspect has been largely disregarded in the literature on social insects, despite early observations that flight velocity of outgoing (unladen) honey bees depends on the concentration of the sugar solution they collect (von Frisch and Lindauer 1955). In this study, however, the increase in velocity of workers recruited to richer sugar solutions depended on the information about food quality they received from a single recruiting ant, because they had no actual contact with the solution. This increase in speed indicates that recruitment signals do transmit graded information about food quality, as known for other ant species (Hangartner 1969; Jaffé and Howse 1979; Breed et al. 1987). In these studies, however, a positive relationship was found between food quality and either intensity of individual recruiting behavior or number of recruited workers emerging from the nest. In the present one, on the other hand, the individual responses of recruited workers proved to be different after the perception of these graded signals.

The nature of the signals modulating the motivational state of *A. lundi* workers and thus their responsiveness remains to be determined. Differences in trail-pheromone concentration on the trail may be involved. It is also notable that when the recruiter ant encountered a worker on its way to or inside the nest, it stopped and displayed conspicuous antennal beats and palpations with its forelegs, to which the nestmate responded by following the chemical trail to the food source. The use of tactile stimulation and stridulation as modulatory signals, which are known to enhance recruitment in other ant species (Markl and Hölldobler 1978; Hahn and Maschwitz 1985; Baroni-Urbani et al. 1988), cannot therefore be excluded. Whatever the nature of the signals involved, the information obtained by recruited workers influenced not only their energy investment per unit time during running, i.e. the power output, but also modulated their individual evaluation of resource quality. For workers collecting standardized sweet-discs, their evaluation was manifested as a higher percentage of trail-layers, the richer the food source about which they have been informed (Table 1). This difference in responsiveness to the same stimulus (a given sweet-disc) can therefore be attributed to variations in the worker's motivational state as a result of the information they received during recruitment. When they encountered non-sugared discs, on the other hand, they did not reinforce the chemical trail at all (Table 1). These facts indicate that workers' own evaluation of resource quality clearly plays a role during decision-making, but recruiting signals can modulate the response thresholds. Note that changes in velocity observed in Fig. 2, where both curves have approximately the same shape but a different position along the ordinate, are in this sense only attributable to differences in the information workers obtained during recruitment. Effects of orientation experience on speed of workers running along the narrow bridge are unlikely. Harrison et al. (1989) found that *Paraponera clavata* workers with experience on a specific foraging route travelled significantly faster than workers unfamiliar with the route. If orientation experience did have an effect on the speed of *Acromyrmex lundi* ants, reduced speeds would be expected for outbound, unexperienced workers, which was not observed during the experiments.

The observed decrease in speed after the collection of a non-sugared paper disc (Fig. 1), which could be intuitively attributed to an effect of the load carried, seems to result from a reduced motivation of workers to carry such a material when they have been informed about a presumably higher-quality resource (sugar solution). That the load itself had no effect on velocity was demonstrated when workers recruited to the same sugar solutions collected sweet-discs of the same weight. In this situation, no reduction in velocity was observed (Fig. 2). The reduction in speed suggests therefore that workers, through the information received during recruitment, may have expected to find a resource of a given quality, and their expectation was not confirmed by the collection of a non-sugared disc. Note that even when workers were recruited to a sugar concentration of 50%, to which they ran with the highest speed recorded (Fig. 1), they never reinforced the chemical trail after the collection of a standard, non-sugared disc, and their velocity was lower after disc collection. Those that found sweet-discs of the same weight (Fig. 2), however, reinforced the trail (Table 1), and showed no reduction in speed. The extreme situation was observed for workers recruited to the most dilute solution, presumably the least motivated if their speed is used as the criterion of readiness to participate in foraging. They refused to pick up the non-sugared discs, even when the same discs were collected under other recruitment intensities. The demonstration that *Acromyrmex lundi* workers learn odors as food signals (Roces 1990a) and that they reinforce the chemical trail on their first way to the source when perceiving this odor during recruitment (Roces, unpublished; similar trail-laying responses of workers orientating towards an odor source have been reported by Littledyke and Cherrett 1978) also suggests that workers have a "search image", in this case determined by learned cues, of the resource to be found.

Changes in the workers' motivational state that depend on differences in resource quality are also suggested from measurements in honey bees collecting at different flow rates of sugar solution (Núñez 1974; Balderrama et al. 1992) or solutions of different concentrations (Schmaranzer and Stabentheiner 1988; Stabentheiner and Hagmüller 1991). Free-flying bees showed an increased metabolic rate at the food source, or reached higher thorax temperatures while dancing in the hive, the more profitable the food source they visited. However, in these studies bees had been trained and had therefore some direct experience of the food source, where their stable performance was under scrutiny. In the present study, on the other hand, the behavior of recruited workers that had no contact with the food source was considered. While for the first studies changes in the motivational state resulted from an individual evaluation of food quality, in the present one they depended on the information received from the first successful recruiter, the only individual that made contact with the sugar solution.

It is perhaps worthwhile to comment on the load capacity of leaf-cutting ant workers, measured as burden [$B = (\text{ant mass} + \text{load mass})/\text{ant mass}$; Rissing 1982], and the possible effects of load on speed. While burden of *Atta* workers can reach values of 7.5 or more, most workers cut and carry leaf fragments giving mean burdens of c. 3.5 (Rudolph and Loudon 1986; Waller 1989). Owing to their reduced leg allometry, *Acromyrmex* workers cut relatively smaller fragments, reaching mean burdens near 2 (calculated from data of Fowler 1979). While effects of larger burdens on velocity may exist and be important in *Atta* workers (Lutz 1929; Rudolph and Loudon 1986; Shutler and Mullie 1991; but no relationship was found by Lewis et al. 1974 or Wilson 1980), burdens up to 2.1 used in the present study caused no reduction in speed in *Acromyrmex* (Fig. 2). On the other hand, it should also be considered that most measurements in *Atta* workers have been made on active field foraging trails, where workers may be in a steady-state phase of their foraging cycle and therefore presumably informed about resource characteristics. In the present study, workers were in a transient phase, at the beginning of trail formation. It is an open question whether differences in motivation between steady-state and transient conditions could modulate the response of ants to variations in load size.

The preliminary estimates of travel costs in *Acromyrmex lundi* showed that, despite the higher velocity and increased metabolic rate of the more motivated workers (unladen or laden), they made an energy investment per trip roughly similar to that of the less motivated workers, which ran slower. These calculations do provide the first tempting insights into the foraging energetics of an ant species under different conditions of foraging motivation, suggesting that workers' energy output per trip was kept roughly constant, independent of travel speed.

Why do recruited workers run faster, when they have been informed about a richer source? The adaptive value of this response could intuitively be assigned to the importance of a rapid transmission of information about a newly discovered food source, since workers arriving earlier at the nest can induce nestmates to follow the trail, for instance via tactile stimulation. At the initial phases of trail development, time-saving would be of great importance in order to monopolize the food source as soon as possible. The evaluation of resource quality by recruited workers and therefore the probability of reinforcing the chemical trail were in part dependent on the information they received, i.e., recruits seemed to rely partially on the decisions of the first successful ants to amplify a recruitment process. It has recently been shown that *Acromyrmex lundi* workers recruited to rich food sources cut smaller fragments than those recruited to poorer ones (Roces and Núñez 1993), although both groups found the same standard material at the source. This behavior, unexpected from an individual point of view, also indicates that, in the initial phases of trail development, workers relied in part on the decisions of the first successful recruiter worker. By cutting smaller fragments, they saved time at the source and ran back sooner to inform about it through reinforcement of the chemical trail (Roces and Núñez 1993), a decision-making system that would ensure a rapid build-up of workers to exploit the discovered source.

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References

Balderrama NM, Almeida de Balderrama LO, Núñez JA (1992) Metabolic rate during foraging in the honey bee. J Comp Physiol B 162:440–447

Baroni-Urbani C, Buser MW, Schilliger E (1988) Substrate vibration during recruitment in ant social organization. Insectes Soc 35:241–250

Beckers R, Deneubourg JL, Goss S (1992) Trail laying behaviour during food recruitment in the ant *Lasius niger* (L.). Insectes Soc 39:59–72

Breed MD, Fewell JH, Moore AJ, Williams KR (1987) Graded recruitment in a ponerine ant. Behav Ecol Sociobiol 20:407–411

Cherrett JM (1972) 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

Fowler H (1979) Environmental correlates of the foraging of *Acromyrmex crassispinus*. Cienc Cult 31:879–882

Frisch K von, Lindauer M (1955) Über die Fluggeschwindigkeit der Bienen und über ihre Richtungsweisung bei Seitenwind. Naturwissenschaften 42:377–385

Fuchs S (1976a) The response to vibrations of the substrate and reactions to the specific drumming in colonies of carpenter ants (*Camponotus*, Formicidae, Hymenoptera). Behav Ecol Sociobiol 1:155–184

Fuchs S (1976b) An informational analysis of the alarm communication by drumming behavior in nests of carpenter ants (*Camponotus*, Formicidae, Hymenoptera). Behav Ecol Sociobiol 1:315–336

Hahn M, Maschwitz U (1985) Foraging strategies and recruitment behaviour in the European harvester ant *Messor rufitarsis* (F.). Oecologia 68:45–51

Hangartner W (1969) Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). Z Vergl Physiol 62:111–120

Hangartner W (1970) Control of pheromone quantity in odor trails of the ant *Acanthomyops interjectus* Mayr. Experientia 26:664–665

Harrison JF, Fewell JH, Stiller TM, Breed MD (1989) Effects of experience on use of orientation cues in the giant tropical ant. Anim Behav 37:869–871

Hölldobler B (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav Ecol Sociobiol 1:3–44

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

Littledyke 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

Lutz FE (1929) Observations on leaf-cutting ants. Am Mus Novit 388:1–21

Markl H, Hölldobler B (1978) Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). II: Vibration signals. Behav Ecol Sociobiol 4:183–216

Moser JC, Blum MS (1963) Trail marking substance of the Texas leaf-cutting ant: source and potency. Science 140:1228

Núñez JA (1974) Metabolism and activity of the worker bee. In: Harnaj V, Schwindt-Escalante O (eds) Proceedings of the 24th Apimondia International Apiarist Congress. Apimondia Ediciones, Buenos Aires, pp 298–299

Rissing SW (1982) Foraging velocity of seed-harvester ants, *Veromessor pergandei* (Hymenoptera: Formicidae). Environ Entomol 11:905–907

Roces F (1990a) Olfactory conditioning during the recruitment process in a leaf-cutting ant. Oecologia 83:261–262

Roces F (1990b) Leaf-cutting ants cut fragment sizes in relation to the distance from the nest. Anim Behav 40:1181–1183

Roces 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

Schmaranzer S, Stabentheiner A (1988) Variability of the thermal behavior of honeybees on a feeding place. J Comp Physiol B 158:135–141

Shutler D, Mullie A (1991) Size-related foraging behaviour of the leaf-cutting ant *Atta colombica*. Can J Zool 69:1530–1533

Stabentheiner A, Hagmüller K (1991) Sweet food means "hot dancing" in honeybees. Naturwissenschaften 78:471–473

Waller DA (1989) Size-related foraging in the leaf-cutting ant *Atta texana* (Buckley) (Formicidae: Attini). Funct Ecol 3:461–468

Wilson EO (1962) Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). Anim Behav 10:134–163

Wilson EO (1980) Caste and division of labor in leaf-cutting ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimization of leaf cutting. Behav Ecol Sociobiol 7:157–165