Resource Assessment, Recruitment Behavior, and Organization of Cooperative Prey Retrieval in the Ant *Formica schaufussi* (Hymenoptera: Formicidae)

Simon K. Robson[1,2] and James F. A. Traniello[1]

Foragers of the ant Formica schaufussi *recruit nestmates to large anthropod prey and cooperatively transport the prey to the nest. The size of the group of ants retrieving prey is significantly correlated with the prey mass at the point at which the retrieval group reaches the nest entrance. To understand the mechanism involved in this "size matching" process, the regulation of retrieval group size was investigated by examining the modulatory role of trail pheromones in recruitment communication and the behavioral processes that might adjust retrieval group size to prey mass. Laboratory studies of hindgut, poison, and Dufour's gland extracts showed that the contents of the hindgut, which was determined to be the source of trail pheromone, induced recruitment and orientation behavior in ants and regulated the recruitment response of ants in the absence of any other communication signal. However, chemical mass communication alone did not appear to explain the regulation of retrieval group size. Scout ants assess whether to collect prey individually or recruit nestmates to group-retrieve 100-, 200-, or 400-mg prey but did not vary group size in relation to either the prey mass or the presence of interspecific competitors once the decision to initiate group retrieval was made. The number of recruits leaving the nest was independent of these factors and first matched prey mass during prey transport, possibly through a process of differential individual response to immobile versus mobile prey items. Unpredictable factors such as prey resistance to movement and rapidly changing degrees of interspecific competition may preclude scouts from fine-tuning the retrieval group size before it reaches the prey.*

[1] Department of Biology, Boston University, Boston, Massachusetts 02215.
[2] To whom correspondence should be addressed at Department of Zoology, James Cook University, Townsville, QLD 4811, Australia. e-mail: Simon.Robson@jcu.edu.au.

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INTRODUCTION

Social insect colonies typically exist within highly diverse resource environments, and the temporal, spatial, and size-frequency distribution of food resources may vary widely within the foraging range of a single colony (Visscher and Seeley, 1982; Traniello, 1989; Traniello and Beshers, 1991). To maximize the efficiency of food collection, foraging effort should be adjusted according to such variability. Indeed, colonies seem able to modulate foraging behavior in an adaptive manner in response to such factors as variable resource distributions (Wilson, 1962; Taylor, 1977; Franks and Fletcher, 1983; Franks, 1989; Seeley, 1989a, b; Seeley et al., 1991; Traniello et al., 1992), foraging risks (Nonacs and Dill, 1990, 1991), and competition (Hölldobler, 1976; Traniello, 1989; Traniello and Robson, 1995).

In ants, the modulation of foraging effort has been considered predominantly with respect to resource quality and distribution and the nature of the competitive environment (Hölldobler and Wilson, 1990). At the individual level, scouts may encounter food items, assess their energetic value, and convey relevant information to the colony to induce cooperative foraging through the recruitment of nestmates. The regulation of recruitment can occur by the scout either controlling directly its own chemical recruitment stimuli or using an additional modulatory signal to modify the effect of a prior recruitment stimuli (Hangartner, 1969; reviewed by Hölldobler and Wilson, 1990). At the colony level, the allocation of foragers to a food source often reflects the dynamics of a mass-recruitment system, rather than an individual assessment and decision per se. Thus, the species-specific foraging patterns of Eciton army ants and the trunk trails of the seed-harvesting ant Messor pergandei can be viewed as colony-level behaviors regulated by the physicochemical properties of pheromones, rather than the actions of individuals with a "global awareness" of food distribution patterns (Goss and Deneubourg, 1989; Deneubourg et al., 1989). Foraging regulation can emerge through collective action, rather than at the direction of single individuals (Deneubourg and Goss, 1989; reviewed by Traniello and Robson, 1995).

The regulation of foraging effort by mass communication in the fire ant Solenopsis invicta demonstrates the interactions between individual and collective behavior. S. invicta scouts can perceive differences in sucrose concentrations and modify the degree and pattern of sting extrusion and the rate of pheromone deposition in their recruitment trails accordingly. Nestmate response is dependent upon trail pheromone concentration (Hangartner, 1969) but is also moderated by colony satiation (Sorenson et al., 1983, 1985), with the resultant colony-level foraging patterns reflecting the physicochemical attributes of pheromone evaporation and diffusion (Wilson, 1962; Deneubourg and Goss, 1989).

Resource assessment and the organization of recruitment behavior in group retrieving species have received less attention (Markl and Hölldobler, 1978;

Hölldobler et al., 1978). Cooperative prey retrieval involves two or more individuals together transporting a food item that could not be collected by a single individual working alone. Group retrieval has been described in swarm-raiding species such as Eciton army ants, in which large numbers of individuals attack and dismember prey and small groups carry it to the nest (Franks, 1986). In other ant species a scout finding a large prey item returns to the colony and recruits nestmates, as is the case in Aphaenogaster cockerelli and Formica schaufussi (Hölldobler et al., 1978; Traniello and Beshers, 1991). Studies of the organization of group retrieval in swarm-raiding species have tended to concentrate on the composition of retrieval groups (Schneirla, 1971; Moffett, 1987; Moffett, 1988a, b) and the existence of teams in polymorphic species (Franks, 1986). Research on group-retrieval behavior in non-swarm-raiding species has focused on the analysis of the signals used in the formation of retrieval groups (Markl and Hölldobler, 1978; Hölldober et al., 1978; Hölldobler, 1983), the mechanics and coordination of cooperative prey transport (Sudd, 1960, 1963; Chauvin, 1968; Meyer, 1970; Chauvin, 1971) and the energetic and competitive significance of group versus individual retrieval (Traniello and Beshers, 1991). In the present paper we examine how cooperative retrieval effort in Formica schaufussi is regulated to match resource quality, by combining laboratory studies of the pheromonal basis of trail communication with field studies of group retrieval in response to varying prey sizes. Because the foraging ecology of F. schaufussi is well understood (Traniello, 1987a, b, 1988; Traniello and Beshers, 1991), we chose this species as a model system to study the behavioral organization and regulation of cooperative prey retrieval groups and its ecological significance.

Group retrieval in the ant Formica schaufussi appears to involve an initial assessment of arthropod prey by a scout ant, which then returns to the colony and recruits a group of workers to transport the prey back to the nest cooperatively. The size of the retrieval group, measured at the point at which the carried prey reaches the nest entrance, is significantly correlated with prey mass (Traniello and Beshers, 1991), but the process by which group size is regulated is not understood. For example, does the individual scout discovering the food determine the appropriate retrieval group size required and regulate recruitment accordingly? Or alternatively, do scouts simply communicate the presence of a "large-prey item" to the colony, with group size becoming matched to prey size through the interaction of individual recruits once they arrive at the prey?

METHODS

Study Species and Field Site

Formica schaufussi is an omnivorous North American temperate zone ant that nests in the soil. Colonies of F. schaufussi were studied in a sparsely

vegetated field/forest transitional habitat at the Concord Field Station of Harvard University in Bedford, Massachusetts. At this site *Monomorium minimum*, *Lasius neoniger*, *Myrmica americana*, *Tetramorium caespitum*, and other *Formica* species are sympatric and show considerable overlap in nesting and feeding habits (Traniello, 1987b). Observations of recruitment behavior occurred in the field between 0800 and 1300 h, from May through August of 1991 and 1992, during peak diurnal foraging activity of *F. schaufussi* at this locality (Traniello, 1987b). Queenright colonies for laboratory studies of chemical recruitment communication were collected during early summer, 1991.

Prey Mass and Retrieval Dynamics

Foragers from a total of three distinct colonies were used through the course of field study. Because there was a considerable overlap in the foraging ranges of neighboring *F. schaufussi* colonies, focal ants were followed as they left the nest entrance to avoid confusion over the colony origin of an individual. When scouts moved 100 cm from the nest entrance they were offered a freshly killed (by freezing) cricket (*Acheta domestica*) weighing either 100, 200, or 400 mg. Prey items of these sizes fall within the range tyically encountered by *F. schaufussi* (Traniello and Beshers, 1991). Each scout was marked on the gaster with a drop of Testors paint and its behavior recorded. Ambient temperature was recorded using a bulb thermometer placed on the soil surface.

A scout was recorded to have retrieved prey as an individual if it moved the prey at least 10 cm during the first 300 s following its discovery, did not abandon the prey to forage elsewhere, or did not return to the colony to recruit nestmates. A scout was considered to have initiated group recruitment if it returned to the colony without the prey and subsequently emerged from the colony with nestmates. If a scout returned to the nest and initiated recruitment, we measured the following temporal aspects of the scout's behavior: the time spent at the prey prior to leaving, the velocity at which it returned to the nest (homing velocity), and the time spent within the nest prior to returning to the prey. Trail-laying (touching the tip of the gaster to the substrate) while returning to the colony, "fast running" by the scout [rapid departures and returns to the prey, comprising short, looping paths (Hölldobler, 1971; Traniello, 1977)], and the presence of workers of competing ant species near or on the prey were also recorded. Fast running usually occurred within 10 cm of the prey. If recruitment from the colony occurred, the following aspects of group dynamics were recorded: the size of the recruitment group leaving the nest with the scout and moving toward the prey, the size of the recruitment group reaching at least 50% of the distance to the prey (i.e., 50 cm from the colony), the size of the recruitment group reaching the prey, and the velocity at which the first member of the recruitment group reached the prey (return velocity). To measure retrieval

dynamics, the time at which prey transport first began after the arrival of the recruited group and the group size at the initiation of prey movement were recorded. With reference to the group behaviors associated with foraging, we use the terms "recruitment" and "retrieval" to distinguish the process of individuals leaving the colony and moving toward the prey versus the behavior of individuals once they arrive at and transport the prey back to the colony.

Observations were terminated if a scout (1) remained at the prey in excess of 300 s without initiating individual or group retrieval; (2) left the prey and failed to locate the nest entrance within the next 300 s (by either moving away from the colony or simply appearing to be unable to find it); (3) returned to and remained in the colony for longer than 180 s; or (4) was unable to relocate the prey after leaving the colony within 180 s. Data used to describe the dynamics of recruitment and group retrieval did not include trials in which observations were terminated at any stage.

Experimental Analysis of Chemical Recruitment Communication

Laboratory analysis of trail pheromone properties used two *F. schaufussi* subcolonies, each comprising approximately 300 workers and 3 or 4 queens, respectively, housed in 14.5-cm-diameter petri dishes placed in two 90 × 45-cm arenas. These colonies were originally a single polygynous colony. Pheromone extract solutions were prepared from the hindgut, poison, and Dufour's glands by dissecting the glands from live workers and crushing five glands of each type in 50 μl of 80% ethanol in a 3-ml Kontes extract vial. Extracts and control solutions (80% ethanol) were prepared each day an assay was conducted and stored on ice before use. Ten microliters of solution was deposited with a Hamilton 701-N microsyringe onto a sheet of paper along a 50-cm-long S-shaped trail drawn out from the nest entrance. During the next 5 min, the recruitment and orientation responses (the number of ants leaving the colony and the distance each ant followed by the trail) were recorded by lightly marking with a pencil the distance traveled. For each gland extract, trials were replicated 20 times (10 replicates with each subcolony). Colonies were deprived of food for between 5 and 10 days prior to trail pheromone assays to intensify the recruitment response.

Hindgut pheromone concentration effects on recruitment and trail following were studied in a single subcolony of *F. schaufussi*. Solutions of 100, 50, 25, and 12.5% hindgut pheromone extract were prepared by crushing six hindguts in 60 μl of 80% ethanol to form a stock 100% solution, then serially diluting 30 μl of this solution with 30 μl of 80% ethanol through three steps. Each concentration was tested a total of eight times. Colonies were food deprived for from 5 to 15 days prior to each experiment to examine the relationship between colony satiation and individual response, and the solutions were presented in randomized order on each day.

RESULTS

Scout Behavior in Relation to Prey Mass

Scouts that located prey either retrieved the prey individually or returned to the colony and initiated group recruitment. The probability that a scout initiated group recruitment increased with prey mass. A scout initiated group recruitment in only 1 (0.3%) of 34 trials if it had discovered a 100-mg prey, 34 (45.3%) of 75 trials for a 200-mg prey, and 42 (95.5%) of 44 trials for a 400-mg prey. When group recruitment was initiated, however, the behavior of a scout during the food discovery and prey assessment stage was not significantly influenced by prey mass (Table I). Because 100-mg prey induced group recruitment and retrieval on only a single occasion, statistical comparisons include scout responses to only 200- and 400-mg prey. The data in Table I were pooled from all three colonies because there were no significant between-colony effects on scout behavior (two-way ANOVA, $P > 0.05$). The time for which the scout remained at either a 200-mg or a 400-mg prey and the velocity at which the retrieval group returned to the prey were influenced by ambient temperature but did not vary significantly with prey mass once temperature effects were controlled for [two-way ANCOVA, $F = 0.21(1,17)$, $P = 0.654$, and $F = 0.00(1,9)$,

Table I. Influence of Prey Mass on the Resource Assessment Behavior, Recruitment Behavior, and Locomotion of Scout Ants During the Initiation of Group Retrieval in the Field[a]

	Prey mass (mg)			
	100	200	400	Prob.
Time spent at prey (s)	93.0	165.8 ± 64.3	131.2 ± 68.8	0.654[b]
	(1)	(27)	(41)	
Probability of ''fast running''	0.0	0.6	0.5	0.340[c]
	(1)	(28)	(36)	
Homing velocity (cm s^{-1})	2.6	3.7 ± 1.9	3.6 ± 2.0	0.814[d]
	(1)	(30)	(38)	
Probability of trail-laying	1.0	1.0	0.9	0.460[c]
	(1)	(6)	(14)	
Time spent in colony (s)	10.0	20.0 ± 15.4	16.8 ± 8.8	0.612[d]
	(1)	(26)	(35)	
Return velocity (cm s^{-1})	2.8	2.6 ± 1.8	2.8 ± 1.2	0.976[b]
	(1)	(23)	(30)	

[a]Scout behaviors are listed in the approximate sequence in which they occur. Statistical analysis between 200- and 400-mg prey only. Mean ± SD, sample size (n).
[b]Two-way ANCOVA.
[c]G test.
[d]Two-way ANOVA.

P = 0.976, respectively]. The probability of "fast running" by the scout [G = 1.16(1), P = 0.340], the velocity at which the scout returned to the colony [two-way ANOVA, F = 0.06(1,62), P = 0.814], the probability that the scout trail-layed while returning to the colony [G = 0.74(1), P = 0.460], and the time spent in the colony [F = 0.26(1,55), P = 0.612] were not significantly influenced by either temperature or prey mass.

The probability that the scout would display fast running while at a 100-, 200-, or 400-mg prey (n = 132) was not significantly influenced by whether the scout retrieved the prey individually (Prob. = 0.37) or by group retrieval [Prob. = 0.43, G = 0.50(1), P = 0.450]. However, when the probability of fast running was considered separately by retrieval method (individual or group), there was a significant relationship between prey mass and the probability of fast running during individual retrieval [G = 17.22(2), P < 0.01]. The scout displayed fast running in only 4 (12%) of the 33 individually retrieved 100-mg prey but displayed this behavior on 21 (58%) of the 36 occasions on which a 200-mg prey and 1 (50%) of the 2 occasions on which a 400-mg prey was individually retrieved.

Prey Mass, Recruitment, and Retrieval Group Dynamics

The recruitment of workers from the nest by a scout did not result in a discrete group of nestmates leaving the colony and being led to the food, as has been described for other ants (Hölldobler, 1971). The emergence of the scout from the nest entrance was usually preceded by a number of ants departing in seemingly random directions but not moving more than approximately 5 cm from the nest entrance. The scout then emerged surrounded by more recruits, which, together with some of the individuals that had initially left the nest, moved in the direction of the prey. Additional individuals could also leave the nest and move toward the prey even after the initial group of recruits had reached the food. Although data were collected on the number of individuals that emerged from the nest but remained at the nest entrance, it is the number of recruits leaving the nest with the scout and the changes in the size of this recruitment group as it moves toward the food that are reported here.

The number of recruited ants leaving the nest differed significantly among the three field colonies [two-way ANOVA, F = 6.186(2,61), P< 0.005] but recruitment group size was not significantly influenced by prey mass [F = 0.407(1,61), P = 0.526) (Fig. 1). Colony 3 consistently responded with a greater recruitment response to either a 200-mg (14.8 ± 3.0 recruits, n = 5) or a 400-mg (17.2 ± 4.5 recruits, n = 9) prey than did either Colony 1 (11.4 ± 8.1 recruits, n = 7, and 9.7 ± 2.6 recruits, n = 9) or Colony 2 (9.5 ± 5.2 recruits, n = 18, and 11.5 ± 5.0 recruits, n = 19, respectively; Scheffe's multiple-range test). Compared between colonies and different prey mass (200
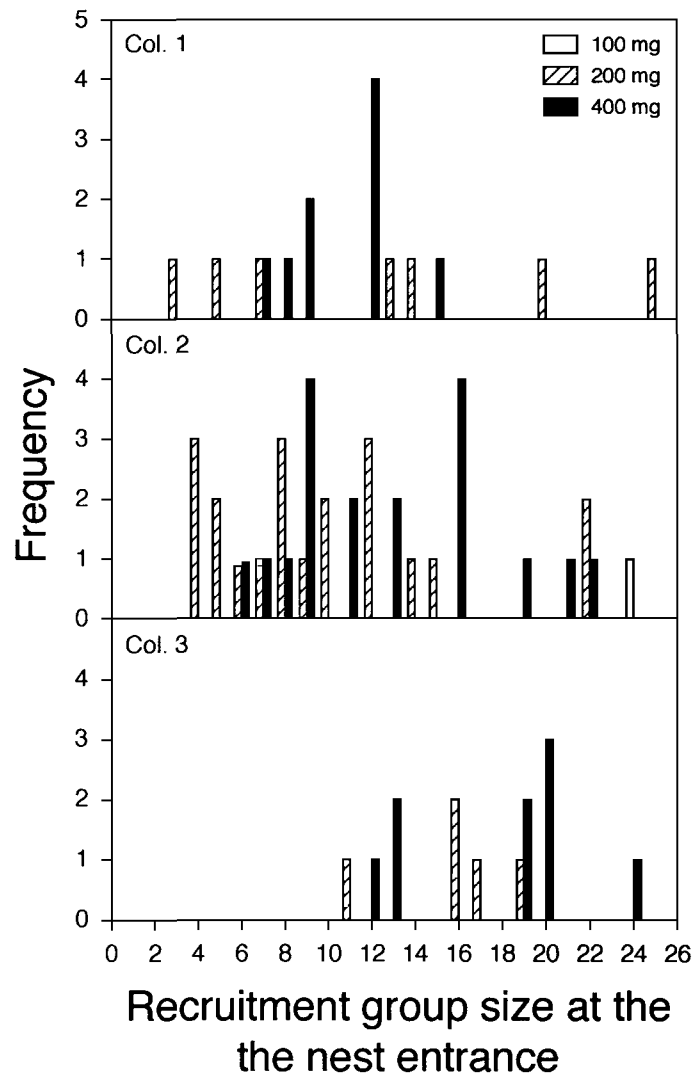
Fig. 1. The relationship between the number of recruits leaving the nest and the prey mass (100-, 200-, or 400-mg prey) in three *F. schaufussi* colonies. Colony 3 showed a greater overall recruitment response, but recruitment intensity was independent of prey mass in all three colonies.

and 400 mg), the size of the recruitment group at the nest entrance showed considerable variability, ranging from 3 to 25 individuals. The single recruitment response to a 100-mg prey appeared to be similar (23 individuals; $n = 1$) (Fig. 1), as it falls within this range.

Recruitment group size decreased significantly as workers moved from the nest entrance to the prey (multiple regression, $t = 8.895(1)$, $P < 0.001$) (Fig. 2). The reduction in group size was again significantly influenced by colony identity ($t = 4.594(1)$, $P < 0.001$) but not prey mass ($t = 1.899(1)$, $P = 0.059$). The reduction in group size was due to individuals leaving the group and either returning to the colony or continuing to move away from the prey. When pooled between colonies and prey types (200 and 400 mg), the mean size of the recruitment group leaving the nest versus that reaching the prey was 11.71 $\pm$ 5.50 ($n = 67$) and 4.45 $\pm$ 4.48 recruits ($n = 69$), respectively, a reduction of approximately 60% of the initial group size. Recruitment group size in response to a 100-mg prey appeared to follow a similar pattern, declining from 23 to 20 individuals at the group moved between the nest and the prey (Fig. 2).

The velocity at which the group of recruits moved from the nest to either 200- or 400-mg prey averaged 2.6 $\pm$ 1.8 and 2.8 $\pm$ 1.2 cm s^{-1}, respectively (Table I) but was not significantly influenced by either prey mass [two-way ANCOVA, $F = 0.00(1,9)$, $P = 0.976$] or colony of origin [$F = 0.24(1,9)$, $P = 0.634$]. The return velocity in response to a 100-mg prey (2.8 s^{-1}) appeared to be similar.

Prey mass significantly influenced the time at which the group first moved the prey and the size of the retrieval group when this movement first occurred (Fig. 3). The data in Fig. 3 were pooled from Colonies 2 and 3, as there were no significant between-colony differences in these measures of retrieval dynamics (two-way ANOVA, $P > 0.05$). The time at which the prey first moved after the arrival of the recruitment group was significantly less for a 200-mg prey (21.1 $\pm$ 17.4 s; $n = 14$) than for a 400-mg prey (42.1 $\pm$ 24.5 s, $n = 19$), [two-way ANOVA, $F = 7.51(1,29)$, $P = 0.010$]. The size of the retrieval group when the prey was first moved was also significantly less for a 200-mg (3.1 $\pm$ 1.4 recruits, $n = 14$) than for a 400-mg (5.6 $\pm$ 3.7 recruits, $n = 19$) [$F = 5.83(1,29)$, $P < 0.05$] prey. This information was not collected on the single occasion on which a 100-mg prey induced recruitment and group retrieval.

Interspecific Competition, Scout Behavior, and Retrieval Dynamics

Interspecific competition occurred in 28 (37.8%; $n = 74$) of the recruitment sequences in which this parameter was recorded in the field. Of these competitive interactions, 21 (75%) involved *Monomorium minimum*, 5 (18%) involved *Lasius neoniger*, and on 2 occasions (7%) both *M. minimum* and *L. neoniger* were
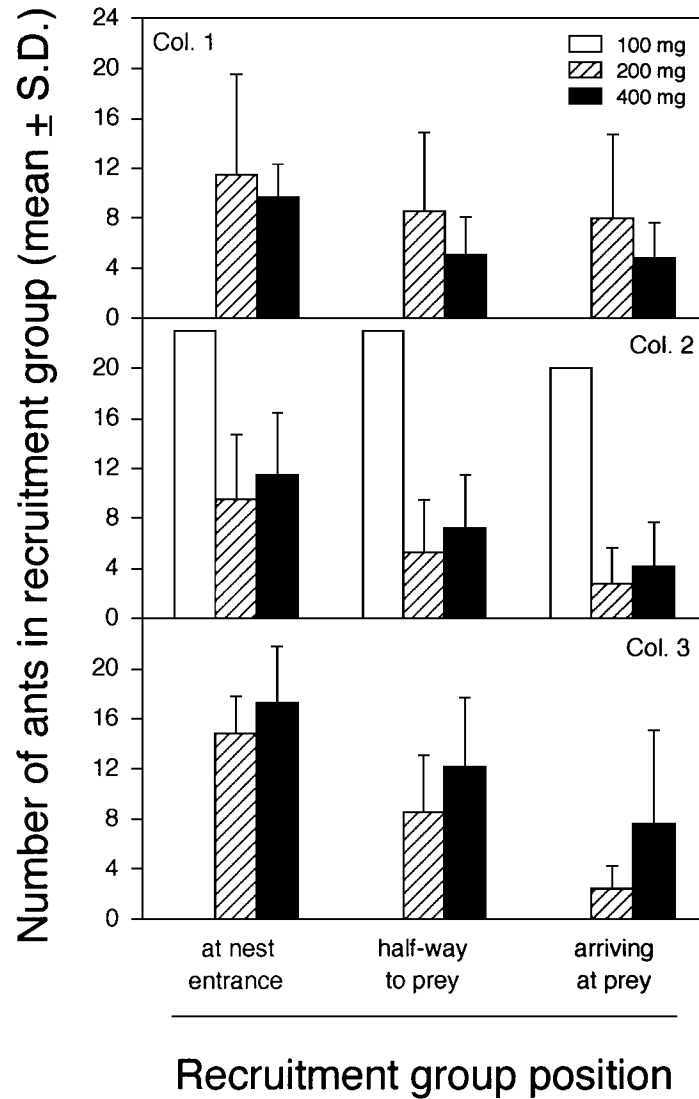
Fig. 2. Changes in recruitment group size as recruits proceeded from the nest to the prey (100-, 200-, or 400-mg prey) in three *F. schaufussi* colonies. The number of workers in the group was recorded at the nest entrance, at one-half the distance to the prey, and at the prey. Recruitment to a 100-mg prey occurred on only a single occasion. Colony and distance significantly effected group size; prey mass did not.

1.0

0.8

0.6

0.4

0.2

0.0

Proportion of initial recruitment group

400 mg Prey 1st moves
(time since arrival = 42.1 sec.)
($\bar{x}$ group size = 5.6 workers)

Recruits
arrive at prey

200 mg Prey 1st moves
(time since arrival = 21.1 sec.)
($\bar{x}$ group size = 3.1 workers)

0   20   40   60   80   100

Time since recruits left colony (sec.)

Fig. 3. Dynamics of cooperative prey retrieval in *F. schaufussi*. Smaller prey commenced transport more rapidly and with fewer recruits than larger prey.

present at the prey. There appeared to be no evidence for species-specific differences in the effect of interspecific competition on retrieval and recruitment of *F. schaufussi* but the low intensity of interaction with *Lasius* precluded statistical tests. The presence of *M. minimum* at the prey affected only one aspect of the behavior of the scout and had no effect on the dynamics of prey retrieval. Of the five measures of scout behavior recorded (feeding time, "fast running" at the prey, homing velocity, time in colony, and probability of trail-laying), homing velocity was the only variable significantly correlated with the presence or absence of *M. minimum* at the prey during the prey assessment stage. Mean homing velocity declined from 3.8 $\pm$ 1.8 cm s^{-1} (n = 24) to 2.2 $\pm$ 0.7 cm s^{-1} (n = 8) when *M. minimum* was present [two-way ANOVA, F = 4.33(1,26), P < 0.05]. There was no effect of colony [F = 0.13(1,26), P = 0.721] or prey mass [F = 0.19(1,26), P = 0.663]. This reduced velocity appeared not to be due to scouts simply moving more slowly. Rather, scouts that had been in contact with *M. minimum* often interrupted their return to the colony to clean themselves of the secretions used by *M. minimum* during competition (Adams and Traniello, 1981) or, in cases of heavy competition, to attack *M. minimum* workers.

The probability that a scout individually retrieved prey or returned to the colony and initiated recruitment was not significantly influenced by the presence

of *M. minimum*. Scouts individually retrieved prey on 12 of 21 occasions (57%) when *M. minimum* were present and on 18 of 24 occasions (75%) when they were not [$G = 1.14(1)$, $P = 0.31$]. Although Colony 3 consistently recruited more individuals to prey [two-way ANOVA, $F = 6.21(1,12)$, $P < 0.05$], there were no significant effects of either prey mass [one-way ANOVA, $F = 2.83(1,12)$, $P = 0.118$] or the presence of *M. minimum* [$F = 1.52(1,12)$, $P = 0.241$] on the recruitment response of this colony. Similarly, compared between colonies the velocity at which recruitment groups returned to the prey [two-way ANOVA, $F = 2.10(1,25)$, $P = 0.160$], the size of the recruitment groups halfway between the nest and the prey [$F = 0.23(1,23)$, $P = 0.634$] and the size of the recruitment group arriving at the prey [$F = 0.12(1,20)$, $P = 0.731$] were all independent of both the presence of *M. minimum* and the prey mass.

Chemical Recruitment Communication

The recruitment and orientation effects of artificial laboratory trails made from extracts of the hindgut, poison gland, Dufour's glands, and control solutions are shown in Table II. The data in Table II were pooled from both sub-colonies, as there were no significant between-subcolony effects on these parameters (two-way ANCOVA, $P > 0.05$). Poison gland and hindgut extracts stimulated significantly more ants to leave the colony [two-way ANOVA, $F = 10.65(3,76)$, $P < 0.001$] than did either the Dufour's gland or the control solutions, which were not different in effect (Scheffe's multiple-range test). The number of ants following the trail for at least 10 cm was significantly greater in response to hindgut solution [$F = 20.72(3,76)$, $P < 0.001$] than it was for any other gland sources. The number of ants following artificial trails comprised of poison gland and Dufour's gland extract were not significantly different from each other or the control solution (Scheffe's multiple-range test). Nestmates leaving the colony oriented along hindgut extract trails for significantly greater distances [$F = 101.98(3,552)$, $P < 0.001$] than for poison and Dulfour's glands extract trails, which were not significantly different from the control solution (Scheffe's multiple-range test).

The relationship between hindgut pheromone concentration and recruitment is shown in Table III. The data in Table III are pooled from both subcolonies, as there were no significant between-subcolony differences (two-way ANCOVA, $P > 0.05$). One-way ANCOVA comparisons of the pooled data were used to test and control for the effect of time since last feeding on the recruitment response of individuals. The time since the subcolonies were last fed significantly influenc d the number of ants following the trail [$F = 4.84(1,34)$, $P < 0.05$] and the mean distance followed [$F = 7.72(1,378)$, $P < 0.01$] but not the number of ants leaving the colony [$F = 2.70(1,34)$, $P = 0.11$]. Hindgut pheromone concentration significantly influenced the number of ants leaving the

Table II. Recruitment and Trail-Following Response to Gland Extracts by Laboratory Colonies of *F. schaufussi*

	Pheromone source*				Prob.
	Hindgut	Poison	Dufour's	Control	
Number of ants leaving colony	$7.9 \pm 4.4^{A,B}$	11.0 ± 6.6^A	4.8 ± 2.9^B	4.0 ± 2.2^B	0.001^a
Number of ants following trail	5.3 ± 3.2^A	1.7 ± 2.8^B	0.8 ± 1.4^B	0.1 ± 0.2^B	0.001^a
Distance followed (cm)	20.6 ± 17.2^A	4.0 ± 8.0^B	3.1 ± 6.1^B	0.4 ± 1.6^B	0.001^b
	(158)	(218)	(99)	(81)	

[a] Two-way ANOVA. Mean ± SD. Each treatment was replicated 20 times.
[b] Two-way ANOVA. Mean ± SD. Statistics based on the total number of individuals (n) that demonstrated trail-following behavior over the 20 experimental replicates.
*Means that are not significantly different for each comparison (Scheffe's multiple-range test; $P < 0.05$) have the same superscript (A or B).

Table III. Concentration-Dependent Effects of Hindgut Trail Pheromone on the Recruitment and Trail-Following Response of Laboratory Colonies of *F. schaufussi*

	Hindgut concentration (%)					
	100	50	25	12.5	0	Prob.
Number of ants leaving colony	13.9 ± 6.1	9.8 ± 4.4	10.0 ± 4.5	9.4 ± 4.0	5.4 ± 1.5	0.008[a]
Number of ants following trail	11.6 ± 5.4	6.6 ± 4.2	5.3 ± 4.4	5.0 ± 3.9	0.3 ± 0.5	0.001[a]
Distance followed (cm)	16.4 ± 14.1	10.8 ± 12.7	7.5 ± 10.5	5.8 ± 7.2	0.4 ± 1.9	0.001[b]
	(111)	(77)	(81)	(72)	(43)	

[a]One-way ANCOVA. Mean ± SD. Each treatment was replicated eight times.
[b]One-way ANCOVA. Mean ± SD. Statistics based on the total number of individuals (*n*) that demonstrated trail-following behavior over the 20 experimental replicates.

colony [F = 3.91(4,34), P < 0.01], the number of ants following the trail [F = 8.93(4,34), P < 0.001], and the mean distance followed [F = 21.65(4,378), P < 0.001].

DISCUSSION

The organization of foraging in ants generally involves communication signals that integrate the behavior of individuals (Hölldobler and Wilson, 1990). Understanding how colonies allocate workers to varying resource distributions and colony needs requires knowledge of the individual behaviors that contribute to the colony-level foraging patterns. In *F. schaufussi* we have attempted to determine if different aspects of the resource and competitive environment are used by individual workers in making decisions about foraging and the mechanism by which such information may be conveyed to the colony. Scouts locating prey assessed whether to retrieve it individually or return to the colony and initiate group recruitment. Although recruitment response was correlated with trail pheromone concentration in laboratory studies and is likely the mechanism by which scouts recruit nestmates, scouts did not appear to use this mechanism to fine-tune group size to the required task. Rather, recruitment response from the nest appeared invariant with regard to prey mass and competitor presence, with the size of the retrieval group becoming matched to the prey mass during the transport of prey.

Individual *F. schaufussi* scouts appeared to assess prey mass in terms of its resistance to retrieval only, with the probability that a scout will return to the nest and initiate recruitment rather than individually retrieve a prey increasing with prey mass. Scouts most likely vary in the absolute prey mass they can individually retrieve, but if scouts initiated recruitment and group retrieval, they did not appear to provide nestmates with information about prey mass. The time for which a scout remained at the prey prior to returning to the colony, the velocity at which it returned to the nest, the probability of trail-laying, and the time for which it remained within the colony prior to leaving with a group of recruits were all independent of prey mass (Table I). We assume that these measurements of scout behavior are accurate indications of how a scout assessed prey quality and whether it transferred information about prey characteristics to nestmates. The data suggest that once the decision to recruit was made, scouts did not discriminate among prey that require cooperative retrieval, because 100-, 200-, and 400-mg prey appeared to invoke the same response by a scout.

The recruitment behavior of the scout also appeared to be independent of competition, even though foraging success is related to the number of recruits and the speed at which they can be brought to the prey by the scout (Traniello and Beshers, 1991). Scouts did not, for example, rapidly leave the prey, return to the nest, and initiate recruitment when *M. minimum* workers were detected,

despite the fact that their chemical interference competition may cause *F. schau-fussi* to lose prey (Adams and Traniello, 1981). The velocity at which scouts returned to the colony was the only recruitment parameter influenced by the presence of the competitor *M. minimum*. Scouts moved more slowly when leaving prey discovered by *M. minimum* but their reduced velocity did not appear to be due to more intense trail-laying. Rather, a scout's return to the nest was often interrupted as it attacked attached *M. minimum* or self-groomed after contacting defensive secretions. This illustrates how chemical interference may influence the recruitment success of *F. schaufussi* and provide *M. minimum* with a competitive edge.

Formica schaufussi scouts that individually retrieved prey did, however, show behavioral differences related to prey mass. These scouts were more likely to display "fast running" behavior when retrieving larger prey. Fast running in *Aphaenogaster* (=*Novomessor*) *cockerelli* scouts acts as a local recruitment stimuli (Markl and Hölldobler, 1978) and may serve the same purpose in *F. schaufussi*.

The regulation of retrieval group size to prey mass did not appear to occur during the initial phase of the recruitment process. Recruitment response from each of the three colonies did not differ with prey mass, with the greater overall recruitment response from a single colony (Colony 3; Fig. 1) probably related to differences in colony size. The velocity at which recruits traveled to the prey and the number of recruits leaving the nest, reaching halfway to, and arriving at the prey did not differ in response to 100-, 200-, or 400-mg prey (Figs. 1 and 2). Similarly, the recruitment response from all three colonies was independent of the presence of mass-recruiting competitors. We therefore could find no evidence to support the idea that retrieval group size is regulated to match prey mass by a scout assessing the prey and conveying information to the colony about the prey mass per se.

Retrieval group size first matched prey mass after recruited ants arrived at the prey, during the process of prey transport (Fig. 3). Smaller prey commenced transport more rapidly and with a smaller number of recruits than larger prey. The reason that the transport of the smaller prey required fewer workers appears to concern friction, but the process by which the number of workers become matched to prey mass is more elusive. A potential mechanism that might underlie the regulation of retrieval group size could involve the differential response of recruits to a moving rather than a stationary prey. Recruits may be less likely to join nestmates and cooperatively transport a moving than a nonmoving prey. Because small prey can be moved with a smaller number of workers, recruits that are not directly involved in prey carriage may leave. Relatively larger prey, however, require more individuals and will continue to stimulate recruits to join the retrievel group until the prey begins to move. This may explain why the

400-mg crickets offered to *F. schaufussi* did not commence transport as quickly as 200-mg prey. It simply took longer for a sufficient number of workers to arrive and overcome frictional forces (Fig. 3). This dynamic process would also serve to regulate the retrieval group size during prey transport, allowing group size to be modulated as the prey moves through microhabitats that vary in their resistance to prey transport.

The fine-tuning of colony recruitment responses by scouts regulating either pheromonal or motor displays is known in a number of ant species and would appear to have been likely in *F. schaufussi*. The pattern of trail pheromone deposition in *Solenopsis invicta* (Hangartner, 1969), *Myrmica sabuletti* (Cammaerts and Cammaerts, 1980), *Formica oreas* (Crawford and Rissing, 1983), *Paraponera clavata* (Breed *et al.*, 1987), and *Pheidole pallidula* (Detrain and Deneubourg, 1997) serves to modulate recruitment response to resource quality. *Pheidole dentata* minors modulate recruitment in response to the competitive environment, regulating the pattern of pheromone deposition from the venom gland to increase the number of majors recruited for colony defense (Wilson, 1976). Motor displays in *Camponotus socius* (Hölldobler, 1971) and *Formica fusca* (Möglich and Hölldobler, 1975) are required for successful recruitment and modulates nestmate responsiveness to the hindgut pheromone of the scout. Stridulation behavior by *Aphaenogaster* (*=Novomessor*) *cockerelli*, *Myrmica scabrinodis*, and *Atta cephalotes* scouts regulates recruitment response, either in a "binary," manner by its presence alone increasing recruitment response, or in a graded manner, where stridulation intensity is directly correlated with recruitment response (Dlussky *et al.*, 1978; Markl and Hölldobler, 1978; Roces *et al.*, 1993).

As is typical for many formicine ants (Hölldobler and Wilson, 1990), recruitment behavior in *Formica schaufussi* is mediated by a hindgut trail pheromone, which can alone induce the recruitment and orientation of workers. Hindgut pheromone concentration can regulate recruitment response in laboratory colonies of *F. schaufussi* (Tables I and II) and therefore might have provided a mechanism for scouts to regulate the actual number of recruits leaving a colony once recruitment was initiated. Certainly the differential response of individuals to varying hindgut pheromone concentrations appears to underlie group recruitment in the field. Scouts use hindgut pheromones to initiate recruitment from the nest, and the reduction in group size as recruits travel from the nest to the prey (Fig. 2) seems to parallel the concentration-dependent trail-following response of workers to artificial hindgut-trails in the laboratory (Table III). Yet scouts do not appear to modulate the specific intensity of the recruitment response of the colony by regulating their own pattern of pheromone deposition. This suggests that, in contrast to species such as *Solenopsis invicta* (Hangartner, 1969), there is not a relatively simple relationship between the structure of

individual trails and the recruitment response. While individual *F. schaufussi* possess the "chemical mechanics" for mass communication and recruitment regulation through pheromones alone, they did not seem to use this process in natural settings.

It is paradoxical that group size was not matched to prey mass at an earlier stage of the retrieval process in *F. schaufussi*, given that retrieval group size is significantly related to retrieval success and the size categories of prey used in this study represent very different energy returns to the colony (Traniello and Beshers, 1991). Larger retrieval groups reduce the probability of prey loss through competition from competitors such as *Myrmica americana*, for example, and the prey delivery rate (mg/s/worker) is more than doubled by group retrieving a 200-mg prey than either a 100-mg or a 400-mg prey item (Traniello and Beshers, 1991). Why don't *F. schaufussi* scouts make some assessment of prey quality and fine-tune their recruitment response? It may be that individual scouts in the field cannot make fine-tuned assessments of the energetic value of prey or the number of recruits required to retrieve it. *Formica schaufussi* scouts may be able to classify prey only in relation to their ability to retrieve it as individuals or groups. The rapid recruitment and monopolization strategies of mass-recruiting competitors such as *Monomorium minimum* and *Myrmica americana* (Adams and Traniello, 1981; Traniello and Beshers, 1991) and microhabitat variation may preclude a scout from predicting the nature of the competitive and physical environment and modulating retrieval group size accordingly. The most effective strategy may be for scouts to recruit a constant number of ants from the colony to all non-individually retrievable prey in the expectation of competition; with subsequent regulation of retrieval group size occurring as a response to realized prey resistance to movement. Certainly *F. schaufussi* scouts are known to be limited in their perceptions and responses to some environmental parameters. Their search behavior, site fidelity, and recruitment response, for example, are determined to a large degree by the type of food reward only. They do not modify their recruitment behavior even when faced with persistent rewards (Fourcassié and Traniello, 1993; Traniello and Robson, unpublished).

The number of *F. schaufussi* workers recruited from the colony declined significantly as the group of recruits travels to the prey (Figs. 2 and 3). What is the value of recruiting so many workers from the colony if the majority of them does not reach the food? It is possible that individuals vary in their ability to follow a pheromone trail and hence a larger number than is required must be induced to leave the colony in order for at least some of them to reach the prey. Alternatively, Pasteels *et al.* (1987) have suggested that the process by which a significant number of mass-recruiting ants lose the trail may be an "adaptive error" that increases the likelihood of the discovery of additional food items. This seems unlikely for *F. schaufussi*, for although group-retrieved prey are a significant component of a colony's overall energy intake, group-retrieved prey

are sporadically encountered by *F. schaufussi* colonies and do not appear to be clumped in space or time (Traniello, 1987b). However, the large number of recruits that fail to reach the prey may represent an "adaptive error" as conceived by Pasteels *et al.* (1987) if it can be shown that they act as an energetically inexpensive way of anticipating and effectively responding to competition.

Recently there has been interest in the concept of "colony integration" and its relationship to the "decision-making properties" of colonies. Such studies have emphasized behaviors of mass-recruiting species, where individual behavioral variance is minimized, individual action appears to be subsumed by the overall colony response, and various aspects of the colony's behavior can be modeled via the physicochemical nature of pheromone deposition, evaporation, and competition (Pasteels *et al.*, 1987; Deneubourg and Goss, 1989; Deneubourg *et al.*, 1989; Aron *et al.*, 1990; Franks *et al.*, 1991; Traniello and Robson, 1995). In these mass-communicating species some aspects of colony behavior can be viewed as arising at the group or colony level, rather than at the level of the individual. Applying these concepts to the foraging organization of *F. schaufussi* asks if the regulation of cooperative retrieval group size represents a centralized process driven through the actions of a single individual, the scout, or arises through a more decentralized process via the actions of the numerous individuals that comprise the retrieval group itself?

Although modulation of retrieval group size is a highly dynamic process involving the interaction of numerous workers, we consider that its organization can be best explained through observations of individual specific behavior during the entire retrieval process, in collaboration with studies of the pheromonal basis of the communication signals involved. Understanding the modulation of retrieval group size in *F. schaufussi* requires study at both the individual and the group level; studies at either level alone only would be insufficient. Individual scouts assessed whether to individually or group-retrieve prey, but the regulation of retrieval group size appeared to occur as a collective process once the recruitment group reached the prey. Scouts did not distinguish between different sizes of non-individually retrievable prey and appeared to convey no information other than the presence of such prey to the colony. A colony's recruitment response did not vary with prey mass or competitor presence, once the scout decided to initiate recruitment. Ultimately retrieval group size was matched to prey mass through the action of individual recruits at the prey while it was being retrieved. Relatively small prey required relatively small-size retrieval groups and began moving more rapidly than larger prey. We suggest that different individual reactions to a moving versus a nonmoving prey (where individuals are more likely to join a stationary retrieval group) may provide the mechanism for what can be perceived as a colony-level process, the regulation of retrieval group size. The demonstration that regulation occurred during the retrieval process, most likely in response to natural parameters such as prey resistance to move-

ment and substrate quality, further argues for the value of examining social dynamic processes within the environment in which they naturally occur.

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