

REGULATION OF RECRUITMENT BY INDIVIDUAL SCOUTS  
IN *FORMICA OREAS* WHEELER  
(HYMENOPTERA, FORMICIDAE)

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SUMMARY

Individual scouts of *Formica oreas* are capable of communicating resource availability, location and quality to nest mates. Recruited foragers can perceive and respond to differences in recruitment stimuli of individual scouts. Significantly more workers followed the path of an individual scout from a more rewarding food source than from a less rewarding food source. These findings suggest recruitment in ant colonies is regulated by recruited workers "weighing" recruitment stimuli of scouts returning from numerous areas about the nest.

RESUME

**La régulation du recrutement par les individus éclaireurs chez *Formica oreas* Wheeler (Hymenoptera, Formicidae).**

Chaque fourmi éclaireuse est capable de communiquer la disponibilité, le lieu et la qualité des ressources trouvées. Les fourmis ouvrières recrutées peuvent, pour récolter ces ressources, reconnaître les différences des stimuli de recrutement de chaque éclaireuse et y répondre. D'une manière significative, davantage d'ouvrières suivent le chemin de l'éclaireuse qui a trouvé la source de nourriture la plus riche. Ces résultats suggèrent que le recrutement dans les colonies de fourmis est déterminé par les ouvrières recrutées qui « savent analyser » les stimuli de recrutement des fourmis éclaireuses revenant à la fourmilière.

INTRODUCTION

The ability of ants to recruit nestmates to a food source is well documented (WILSON, 1962 ; SZELP and JACOBI, 1967 ; HÖLLDOBLER and WILSON, 1970 ; HÖLLDOBLER, 1971 ; HÖLLDOBLER *et al.*, 1978). Recruitment enables a colony

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to collect food efficiently (HÖLLDOBLER and WILSON, 1970; HÖLLDOBLER, 1976; TAYLOR, 1977, 1978; HÖLLDOBLER *et al.*, 1978) and to defend and gain territories (HÖLLDOBLER, 1976; HÖLLDOBLER *et al.*, 1978). Mechanisms to communicate food availability by ants include an impressive array of motor displays and pheromone trails (PARRY and MORGON, 1979). The evolutionary development of recruitment techniques among ants is expected to result in an increase in importance of orienting information contained in a pheromone trail and a decrease in importance of motor displays (HÖLLDOBLER, 1977; TRANIELLO, 1977). Information communicated on recruitment will decrease time and energy spent by colony mates searching for food. Optimally, recruitment should be regulated; i.e. degree of colony response should be a function of net benefit available from a given food source (TAYLOR, 1977, 1978).

Resource quality is postulated to be communicated by a foraging group's "electorate" response: proportion of individuals laying a pheromone trail depends on the quality of food (WILSON, 1962; SZELP and JACOBI, 1967; CHADAB and RETTENMEYER, 1975). Additionally, in *Solenopsis germinata* the amount of pheromone laid by an individual increases with higher food quality (HANGARTNER, 1969). Among those ants using motor displays, intensity of a recruiter's display may increase with net quality of food source. (SZELP-FESSEL, 1970; CAMMAERTS, 1977; SZELP and JACOBI, 1977; TRANIELLO, 1977). The ability of colony members to detect and respond to differences in recruitment stimuli from an individual scout, however, has not been examined in either case (i.e. pheromone trails or motor displays). In this paper we examine regulation of recruitment response in a *Formica oreas* colony presented simultaneously with food sources of differing quality. We present experimental evidence showing that an individual scout communicates sufficient information to regulate recruitment and that colony members can differentiate between recruitment stimuli of individual recruiters.

## METHODS

A queenless colony of *F. oreas* Wheeler housed in a plastic box with nest material was placed in a foraging arena (150 × 60 × 4 cm). Three feeding pedestals (5 cm high) were placed 80 cm from the nest; a small petri dish was placed on each pedestal. Ants gained access to each pedestal by climbing a 12 cm ramp; the three ramps shared a common junction on the foraging arena floor at a small glass plate (3 × 5 cm). An aspirating tube was fitted over each ramp forming a tunnel through which ants had to pass (*fig. 1*).

The number of ants ascending each pedestal was counted for ten minutes before any manipulation. For each recruitment experiment a petri dish received either 4 ml of 1.5 or 0.5 M sucrose solution or was left empty. Field experiments had indicated this species preferred 1.5 M solutions over stronger or more dilute solutions of sucrose (RISSING, unpublished data). Locations of solutions and controls were assigned randomly with the condition that each pedestal had a food source different from the previous experiment and in three consecutive experiments each pedestal received all three food

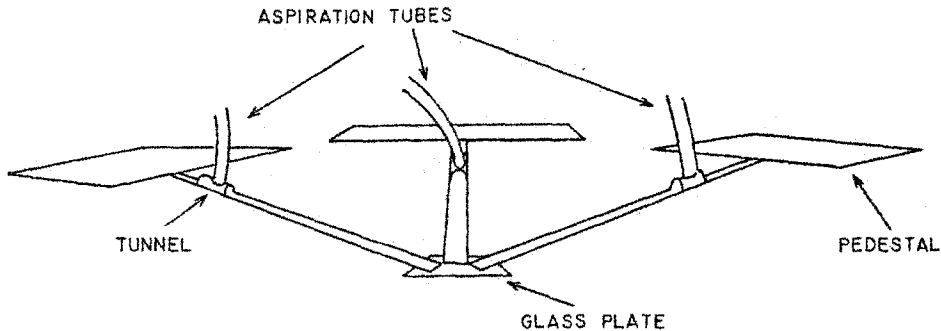


Fig. 1. — Diagrammatic illustration of feeding platforms (legs not drawn). Ramps are equal in length.

Fig. 1. — Illustration des plates-formes (pieds non dessinés). Les rampes sont toutes égales en longueur.

sources. Thus, all pedestals were assigned with equal frequency to each experimental condition so that any affect of geometry (e.g. favoring central pedestal) would be experimentally removed. An experiment was initiated by adding sucrose solutions to the predetermined petri dishes and placing a single ant on each pedestal (by allowing an ant to climb onto a small dowel and transferring her to the pedestal). This required very little time and all ants were usually in place within one minute. These ants were marked (by lightly touching their gaster with paint; causing very little disturbance). Then the ants were allowed to feed on the sucrose solution (if present) and return to the nest. The amount of time each initial scout spent at each food source was recorded. All ants climbing the ramps during the next 20 minutes (after the initial scout had descended) were aspirated and counted. Thus, only the initial scout was able to communicate information regarding the new food source. After each experiment all aspirated ants were returned to the nest; pedestals, ramps and the glass plate were washed with 95 % ethanol and distilled water and returned to their original positions. Several drops of 1.0 M sucrose solution were placed in each petri dish between experiments. Experiments were usually run every other day; a total of 9 experiments were performed.

## RESULTS

Recruited workers differentiated between recruitment stimuli of individual scouts resulting in significantly more ants climbing more rewarding pedestals. Significant differences existed in mean number of ants responding to all treatment conditions (*fig. 2*,  $P < .001$ , Jonckheere Test, HOLLANDER and WOLF, 1973) and between control vs. 0.5 M and 1.5 M vs. 0.5 M ( $P < .05$ , Wilcoxon match-paired signed-rank test, SIEGEL, 1956). These differences were not a function of amount of time spent by the initial scout at its respective food source (i.e. the difference in the departure time from the pedestal); there were no significant differences in this amount of time between the 3 experimental conditions, especially between 0.5 M and 1.5 M

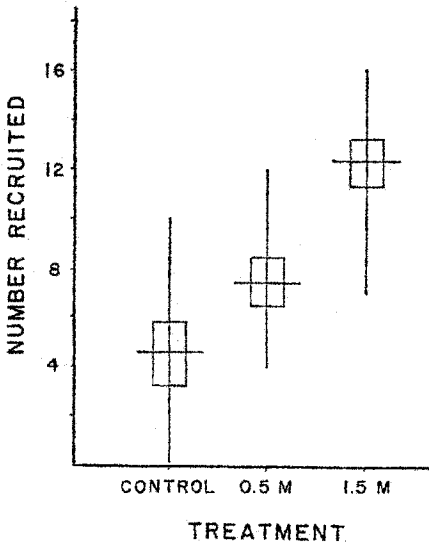


Fig. 2. — Mean number of ants climbing each ramp during 20 minutes following descent of an individual scout. Probability that observed differences between means are due to random effects alone  $< 0.001$  (Jonckheer test of order alternative, HOLLANDER and WOLFE, 1973). Means (horizontal lines),  $+ 1$  S.E. (box), and range (vertical lines).

Fig. 2. — Nombre moyen de fourmis montant chaque rampe pendant les 20 minutes qui suivent la descente d'une fourmi éclaireuse. La probabilité que les différences observées entre les moyennes soient dues au hasard est de moins de 0,001 (voir le test Jonckheer, HOLLANDER et WOLFE, 1973). Moyennes (lignes horizontales)  $+ 1$  E.S. et amplitude de la variation (lignes verticales).

Table I. — Amount of time the initial scouts spent at each food source. Values are means (minutes)  $\pm 1$  SD based on 9 observations (1, 2, 3).

Tableau I. — Temps passé par chaque éclaireuse initiale au niveau de chaque source alimentaire. Les valeurs sont des moyennes (en minutes)  $\pm 1$  DS, à partir de 9 observations (1, 2, 3).

Control (min)	0.5 M (min)	1.5 M (min)
$2.7 \pm 2.1$	$4.4 \pm 2.4$	$4.0 \pm 2.6$

- (1) Probability that observed differences between the 3 means are due to random chance alone:  $P > .20$  (one-way Anova).
- (2) Probability that observed differences between 0.5 M with 1.5 M (pooled) and control is due to random chance alone:  $P < .10$  (t-test, one tailed).
- (3) Probability that observed difference between 0.5 M and 1.5 M due to random chance alone:  $P > .50$  (paired t-test).

sucrose solutions (table I). No significant differences exist between the number of ants ascending the ramps before experiments ( $0.30 < P < 0.50$ , Kruskal-Wallis one way analysis of variance, STEGEL 1956).

## DISCUSSION

Recruitment is expected to be regulated in ant colonies: as net benefit from a given food source increases, the number of workers responding to that source is expected to increase (TAYLOR, 1977, 1978). A variety of condi-

tions will determine quality of any food source to an ant colony including degree of colony starvation, distance to source, size of source, and (especially in liquid feeding ants) concentration of source (HANGARTNER, 1969; HÖLLDÖBLER, 1976; TAYLOR, 1977). Recruitment to food is postulated to be regulated by an "electoral" response, i.e. the number of ants that act as recruiters and lay trail pheromones or perform recruiting displays to a food source is directly related to food source quality (WILSON, 1962; SZELP and JACOBI, 1967; CHADAB and RETTENMEYER, 1975; CAMMEARTS, 1977; HARTWICK *et al.*, 1977; TRANIELLO, 1977). Recruitment may also be regulated by differences in individual motor displays that may vary with quality of the discovered food source (SZELP and JACOBI, 1967; SZELP-FESSEL, 1970; CAMMAERTS, 1977; TRANIELLO, 1977). Our experiments demonstrate that a colony can also correctly regulate degree of its recruitment response based upon the information conveyed by an individual scout.

Regulation of recruitment depends on the communication of resource availability, location and quality. If only resource availability was communicated by individual *F. oreas* scouts, the number of ants arriving at each pedestal (including control) would be equal. If both availability and location were communicated, then more ants would arrive at the sucrose solutions than control; with no differences between the two sucrose solutions. If all the information (availability, location and quality) were communicated, then recruitment rate to each food source should be a function of resource quality, as we observed. Ability of a single ant to communicate this information should reduce the time required for a colony to modulate the intensity of recruitment.

Although experiments were not conducted to test the method of recruitment or communicating information, there is sufficient evidence to indicate that a pheromone trail is involved. The related European species, *Formica rufa* (ROSENGREN, 1971) and many other ants (WILSON, 1971; PARRY and MORGAN, 1979) use pheromone trails in recruitment. More importantly, workers recruited to any of the three food sources had to follow the same general path from nest box to the glass plate approximately 70 cm away. At the glass plate all recruited ants (and any returning scouts) reached a decision point regarding which ramp to climb. Our data indicate these outgoing foragers received sufficient information from scout ants to result in significantly more ants making a "correct" decision and climbing more rewarding ramps. This decision was made without the presence of the initial scout (i.e. the ant placed on the pedestal and marked). Clearly, the most parsimonious explanation of the method of communication would be a pheromone trail. The work of HANGARTNER (1969) suggests a possible mechanism for communication of resource quality by an initial scout: he has shown that "continuity" and intensity of individual *Solenopsis geminata* pheromone trails is dependent upon perceived quality of the discovered food source. It is also possible that recruitment in

*F. oreas* is mediated by some form of motor display (SZELP and JACOBI, 1967; SZELP-FESSEL, 1970; MÖGLICH and HÖLLDOBLER, 1975; CAMMAERTS, 1977; TRANIELLO, 1977), however, we saw no such behavior during observed scout-worker encounters. "Tandem running", a form of recruitment where nest mates follow a recruiter (often in physical contact) to a food source, is unlikely in this case since ants continued to arrive at food sources throughout the 20 min. period and did not arrive in a single "surge", nor were they in physical contact or close proximity to the initial scout if it returned (recall that only the initial scout was allowed to return to the nest once during each experiment, making subsequent "tandem running" scouts impossible).

*Formica oreas* foragers appear capable of perceiving and responding to differences in pheromone trails of individual recruiting nest mates. For this system of recruitment regulation to work, ants must "weigh" the information transferred by several scouts and individual scouts must be similar to each other in their evaluations of quality of food sources they discover. In particular, scouts must be of similar perception of the current nutritional state of the colony as a whole. Such ability appears possible given the high degree of trophic exchange that occurs in ant colonies (WILSON, 1971) especially between scouts and other foragers (WALLIS, 1964). It is not necessary for an individual scout to know the quality of other food sources in use by the colony or being discovered simultaneously by other scouts. The individual scout need know only the general nutritional state of the colony (as likely indicated by its own hunger) and determine the value of any food source it may discover accordingly. Integration of the information collected by the individual scouts regarding resource availability can be performed by the foragers as they come into contact with the recruitment trails of the scouts.

This system of recruitment regulation, especially in colonies of *Formica* spp. which tend to be very populous and forage over large territories (WEBER, 1935; SATHER, 1972; ROSENGREN, 1971), may be very adaptive. One point that deserves further examination is whether recruited forgers can perceive a "mean individual response" on the part of scout ants, i.e. can recruited ants differentiate between several scouts laying weak trails and a single scout laying a strong trail.

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