JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
56(3), 1983, pp. 277–285

The Relation of Recruitment Rate to Activity Rhythms in the Harvester Ant, *Pogonomyrmex barbatus* (F. Smith) (Hymenoptera: Formicidae)

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ABSTRACT: The response of a colony of *Pogonomyrmex barbatus* to bait depends on the activities of the colony at the time bait is offered. Colony activities are temporally patterned within the morning activity period. Both the peak of nest-maintenance work and the onset of the peak of patrolling occur earlier than the peak of foraging. The rate of recruitment to bait is positively correlated with the numbers of ants engaged in nest-maintenance work and patrolling, but, surprisingly, it is not correlated with the number of ants foraging. Thus the stage in the activity period when bait is offered affects recruitment rate.

A colony of harvester ants provides a convenient and intriguing system with which to investigate foraging ecology. Studies of ant foraging ecology make frequent use of two variables. The first is the number of ants foraging at a particular time. In this paper "foraging" means travelling to or from a colony's seed source on a permanent, cleared path. The second variable is rate of recruitment to bait. In contrast to foraging, recruitment is a short-term process. A temporary trail of ants to a new food source builds up, then disappears when the food is gone. "Recruitment rate" is the number of ants per unit time that come to a food source to retrieve the food after it has been discovered. This study examines the relation between recruitment rate and the temporal pattern of foraging and other activities.

Recruitment rate is known to be affected by environmental factors (e.g., presence of other colonies) and characteristics of the food source (e.g., amount, type, density, distance from the nest) (Hölldobler, 1976; Davidson, 1977a, b, 1980), and the hunger level of the colony (Wallis, 1962). However, even after taking these factors into account, some authors have noted a great deal of variability in the recruitment rate of particular colonies (e.g., Hölldobler, 1976). Chew (1976) noted that, at times, actively foraging colonies do not recruit to bait at all.

The recruitment rate of *Pogonomyrmex* colonies has been measured to test hypotheses about interference competition in desert ecosystems (Davidson, 1977b, 1980; DeVita, 1979; Hölldobler, 1976) and to census populations of particular species within the community (Davidson, 1977a; Culver, 1974; Chew, 1977). Taylor (1977) found the "general recruitment level" of *P. occidentalis* to be a significant factor in his optimal foraging model, but he pointed out that recruitment rate had to be "taken as a given which cannot be predicted by our present level of understanding."

The present study examines recruitment rate within the context of other colony activities at the time bait is offered. In previous studies of other aspects of ant

Accepted for publication 15 December 1982.

behavior, the activities of the colony at the time experimental manipulations were performed determined colony response (Gordon, 1983; Meudec and Lenoir, 1982). The following questions are addressed: 1) Is there a temporal pattern in the various activities of the colony's outside work force? Previous studies of daily activity rhythms have measured the numbers of ants entering and leaving the nest (e.g., Bernstein, 1979; Whitford et al., 1976). Daily rhythms in activities other than entering and leaving the nest have been documented but not investigated quantitatively (e.g., Wheeler and Rissing, 1975; Willard and Crowell, 1965; Levieux and Diomande, 1978). 2) Is recruitment rate correlated with any colony activities at the time bait is offered? If so, how is the colony's response to bait related to its activity rhythms?

Methods

STUDY AREA: The study was conducted near the Southwestern Research Station in Portal, Arizona. The morning activity periods of 6 colonies of *P. barbatus* were observed for 20 days in August 1981. Colonies of *P. barbatus* make nest mounds and clear a circular area, about 2 m in diameter, around the mound, called the "nest yard" (Hölldobler, 1976). The colony piles seed husks, grass clippings and other materials into a "midden" on the nest mound. One or more cleared trunk trails radiate from the edge of the nest yard into the surrounding vegetation. Foraging ants travel along these trails for 5–15 m, then leave the trail to gather seeds. Several other species of *Pogonomyrmex* are common near Portal, but the study colonies were located in a 10 m by 70 m plot in which no other species of *Pogonomyrmex* were found.

ACTIVITY RHYTHMS: To determine whether colony activities are temporally patterned, I defined five types of activity and periodically recorded the numbers of ants outside the nest engaged in each one. All activities observed during 20 hours of observation in a 6-day pilot study were classified into five categories (Table 1): 1) foraging, 2) nest maintenance, 3) patrolling, 4) midden work, and 5) convening. Data on activity rhythms were collected by taking a standard walk, routed past each of the study colonies. During each observation of a colony, I recorded: 1) the time and 2) the number of ants within the nest yard engaged in each of the five categories of behavior. Ants outside the nest yard but within 0.3 m of its edge were also counted because patrolling ants were most often in this vicinity. Ants on the foraging trails were not counted. Each observation lasted about 5–10 minutes. The walk was repeated at intervals of 30–60 minutes throughout the morning activity period of the colonies, from about 6:30 a.m. to 11:30 a.m. Thus, each colony was observed four or five times a day. No colony was active on all 20 mornings. I obtained 200 observations of active colonies.

To determine whether colony activities were significantly different from hour to hour of the morning activity period, the numbers of ants in each activity were sorted according to time of observation into 5 one-hour slots beginning at 6:30 a.m. The mean numbers of ants in each activity, in a particular hour slot, were used as observational variables in a multivariate analysis of variance (Timm, 1975). The same analysis was performed using the mean proportions of ants in each activity and in each hour slot. The proportions used in these and subsequent analyses were first subjected to an arcsin transformation (Sokal and Rohlf, 1981). Data from all six colonies were pooled because an analysis of variance which

Table 1. CLASSIFICATION OF COLONY ACTIVITIES

FORAGING	A.	Ants travel directly away from the nest entrance, not carrying anything, on a foraging trail.
	B.	Ants travel directly to the nest entrance carrying a seed or insect bit, on a foraging trail.
NEST MAINTENANCE	A.	Carrying out: Ants come out of the nest entrance carrying something, put it down in the nest yard, and go back into the nest. This usually occurred in groups of 4-10 workers.
	B.	Clearing vegetation: Ants climb in vegetation at edge of nest yard, clip pieces of it off with mandibles.
	C.	Ants open nest entrance at the beginning of activity period by carrying out soil.
	D.	Ants close nest entrance at the end of the activity period by filling it with soil.
PATROLLING	A.	Ant walks with frequent stops and changes of direction, so that overall trajectory is zig-zag, not direct. Abdomen is often bent underneath the thorax. Objects encountered are frequently inspected with antennae.
MIDDEN WORK	A.	Ants pick up objects in the colony midden and move them to some other location in the next yard, such as a newer, smaller midden, or the edge of the nest yard.
	B.	Ants come into the nest yard, not along the foraging trail, bringing small pebbles, and put them down on the nest mound.
	C.	Ants stand on the midden, inspecting it with antennae.
CONVENING	A.	Ants mill around in nest entrance. Frequent antennae contacts between workers.

tested for colony differences as a main effect, and for an effect of interaction between colony and time slot, showed no significant colony differences in the proportion of ants in each activity and time slot.

RECRUITMENT TO BAIT: The following experiments with bait were conducted to determine the effect of colony activities on recruitment rate. Before each experiment the number of ants engaging in each of the five activities in Table 1 was recorded. Then the colony was immediately given a new food source, or "bait," consisting of 2 tablespoons of mixed bird seed, containing millet, milo, and cracked corn, placed on the center of a piece of filter paper 11 cm in diameter. In a given experiment, the bait was placed either at the edge of the nest yard directly outside the midden and not on any trunk trail, or 2–3 m from the nest entrance alongside a trunk trail. The first location was more accessible to midden workers, nest-maintenance workers, patrollers, and conveners than to foragers. The second location was more accessible to foragers than to ants engaged in any of the other four activities. Preliminary experiments showed little or no recruitment to bait placed 3–5 m from the nest yard edge, more than 2 m from a trunk trail. The bait was observed for twenty minutes. The number of seeds carried off the filter paper during each minute was recorded. I made 46 experiments of this kind, never more than once a day on any colony.

Recruitment rate was calculated by dividing the total number of seeds retrieved by the number of minutes required to remove all seeds, using a maximum of 20 minutes. Recruitment rate was equated with retrieval rate so that ants that inspected the bait but left without picking up seeds would not be counted as "recruits."

To determine whether recruitment rate is correlated with the activities of the ants at the time bait is offered, I tested for correlation between the recruitment

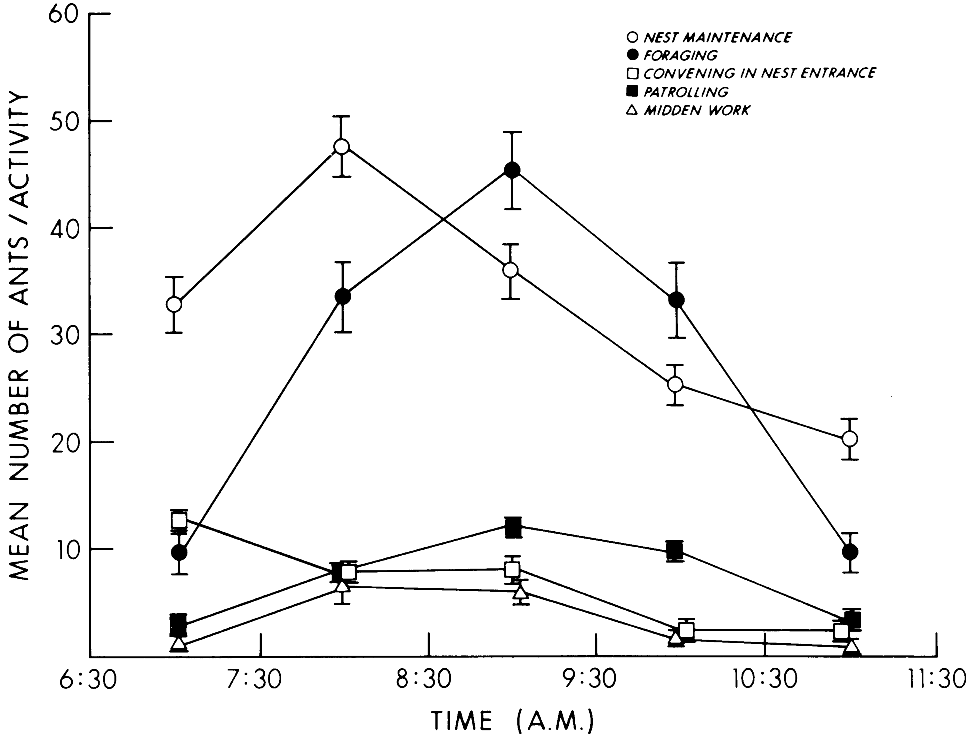

Fig. 1. Each point represents the mean number of ants engaged in the specified activity in the specified hour. Error bars show standard error of the mean (N = 200).

rate and frequency of behavioral categories, using the observations made of colony behavior immediately before the recruitment experiment. A similar analysis was performed using the proportions of ants in each activity. The recruitment rates in the two different locations were compared using a *t*-test.

Results

ACTIVITY RHYTHMS: The temporal patterns of the morning activities of the colonies are shown in Fig. 1. The mean vectors describing the activities of the ants in each hour period were found to be significantly different ($P < 0.001$). The same analysis using the mean proportions resulted in significant differences from one hour slot to another ($P < 0.001$), reflecting a true difference in temporal pattern of colony activities in each hour, which is not an artifact of the total number of ants out of the nest.

Thus the activities of the ants show a clear temporal pattern. The frequencies of nest maintenance and foraging show distinct, successive peaks. Patrolling and midden work show broader peaks of frequency. Most convening takes place at the beginning of the activity period. The colony performs different tasks at different stages of the morning activity period.

RECRUITMENT RATE: Recruitment rate varied between 0 and 21.3 seeds/minute. It was positively correlated with nest maintenance ($r = 0.416$, $P < 0.004$) and patrolling ($r = 0.318$, $P < 0.033$). It was not significantly correlated with any of

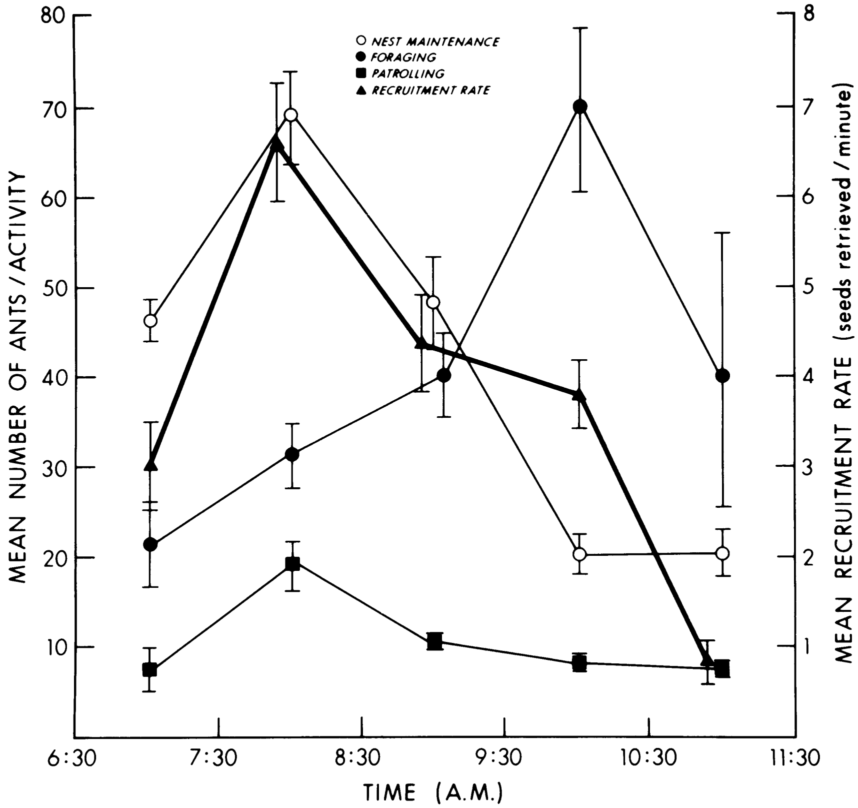

Fig. 2. Mean recruitment rate and mean number of ants engaged in each of three activities, in each hour. Only behavioral observations made immediately before recruitment experiments are included. Error bars show standard error of the mean (N = 46).

the other three behavioral variables, including foraging ($r = -0.102$, $P < 0.501$), or with the total number of ants counted in the nest yard ($r = 0.246$, $P < 0.104$).

A stepwise linear regression showed that a one-variable model using nest maintenance is sufficient to predict the variation in recruitment rate ($P < 0.005$), but patrolling, which with nest maintenance provides the best two-variable model, does not contribute significantly ($P < 0.148$) to a prediction of recruitment rate. However, since patrolling ants were observed to react to bait, I consider the significant correlation ($P < 0.03$) between recruitment rate and patrolling to reflect a true relationship between these two types of behavior.

Figure 2 shows how recruitment rate is related to the colony activity rhythms. Included in this figure are the behavioral data collected before recruitment experiments and the data on recruitment rate, each displayed as a function of time. Figure 2 helps to explain why recruitment rate was correlated with numbers of ants engaged in nest maintenance or patrolling, but not with numbers of ants foraging. The peak in recruitment rate coincides with the peaks in nest maintenance and patrolling, while the peak in foraging occurs later in the activity period.

The peak in patrolling activity is represented as earlier in Fig. 2 than in Fig. 1 due to inclusion of the behavioral observations recorded before recruitment experiments. The larger size of the sample used in Fig. 1 (N = 204 for Fig. 1, N = 46 for Fig. 2) would lead one to expect the curves to be more spread out in Fig. 1, as is the case. Also, it appears that recruitment experiments were performed when the differences between numbers of ants patrolling and foraging were especially pronounced. This was not intentional, but it allows for a clear separation of the effects of patrolling and foraging on recruitment rate.

The analysis using proportions of ants in each activity yielded very different results. Recruitment rate was not significantly correlated with the proportion of ants in any of the five activities or with the total number of ants outside the nest. These results indicate that a minimum number of ants must be engaged in nest maintenance or patrolling before intensive recruitment can take place. Hölldobler and Wilson (1970) showed that *Pogonomyrmex* uses a chemical mass-recruitment system. This indicates that intensive recruitment is elicited when many successive pheromone trails are laid by ants returning to the nest from a food source. The results of the present study show that, even if a relatively large proportion of the colony is engaged in nest maintenance or patrolling, intensive recruitment will not take place unless a sufficient *number* of recruiters is present.

Recruitment rates at the edge of the nest yard and alongside a trunk trail were not significantly different ($P < 0.985$).

Discussion

This study emphasizes that not all of the ants outside the nest are foragers. The significance of the point has not been generally recognized. But it is clear that to determine foraging schedules one should distinguish foragers from other ants. Foraging activity is usually measured by making a periodic count, during a short time interval, of the number of ants leaving the nest (e.g., Bernstein, 1979; Hansen, 1978; Wallis, 1962; Van Pelt, 1966; DeVita, 1979), entering the nest (e.g., Whitford et al., 1975, 1976, 1981), or entering and leaving the nest (Davidson, 1977b; Hunt, 1974). This provides a comprehensive measure of colony activity but a possibly inaccurate measure of foraging activity.

The distinction between foragers and other ants, furthermore, is crucial to the evaluation of parameters in optimal foraging theory, e.g., foraging success, foraging distance, search time, and number of available foragers. For example, several investigators (Hansen, 1978; Whitford, 1978, 1981; Davidson, 1977b; DeVita, 1979) have construed foraging success as the ratio of the number of workers returning to the nest with a food item to the total number of workers returning to the nest. Some of these authors reported remarkably low success rates. Hansen (1978) found that 50% of returning "foragers" did not carry forage items. Whitford (1978) found varying rates of success ranging from 12% to 91%. If workers returning to the nest were not all foragers, this measure of foraging success may be inadequate.

It has long been known that seed-eating desert ants accomplish tasks other than foraging outside their nests. The task most often mentioned is termed "nest work," defined by Wheeler and Rissing (1975) as "removing the excavated material and other refuse from the nest," and similarly defined by Porter and Jorgensen (1981). I distinguish nest maintenance (removing excavated material from the nest) from midden work (sorting material on the surface of the nest mound). This distinction is supported by the results of this study, which indicate that nest-maintenance workers recruit other ants to bait while midden workers do not. Another task, that of scouting or patrolling, has been mentioned by Hölldobler (1976) and Davidson (1977b), who refer to ants that alert the colony to the presence of a new food source as "scouts." The present study indicates that patrollers do recruit other ants to bait.

The low recruitment response of foraging ants to bait may seem paradoxical. It is clear that the result is not simply due to the location of the bait. If proximity determined recruitment rate, foragers would have recruited other ants to bait placed alongside the trunk trail, which they did not, and midden workers would have recruited others to bait placed at the midden's edge, which they did not. Instead, patrollers and nest-maintenance workers recruited other ants to bait in both locations. It may be that foragers do not digress from their trail to an established food source because their search is seed-specific (Rissing, 1981) or even site-specific (Herbers, 1977).

The results of this study suggest that individual ants fall into three classes: those that forage but will not recruit others to bait (foragers), those that do other tasks but will recruit to bait (patrollers and nest-maintenance workers), and those that neither forage nor recruit others to bait (midden workers and convening ants). These results raise interesting questions about the behavioral plasticity of individuals of *P. barbatus.* Experiments with marked individuals are in progress to investigate the mechanisms at the individual level which led to the observed correlations. However, whatever the individual mechanisms, the relation between colony activities and recruitment rate is of clear methodological significance.

Research that uses measurements of recruitment rate should take behavioral factors into account. It is essential to know which tasks are correlated with recruitment rate, and how these tasks are ordered within an activity period. For example, recruitment rate may be used as a measure of interference competition by determining which of several species in a community can recover more of a bait. However, bait may be offered at a time when species A will recruit while species B, though active, will not. At a different time, species B might recruit while species A, though active, would not. To ensure that recruitment rate is sampled in both these situations, the investigator should understand the relation between recruitment rate and the activity rhythms of the species being studied.

In interpreting this study, it should be remembered that recruitment rate has not been shown to depend directly on clock time. In fact, the time in the activity period that particular colonies show peak recruitment is known to vary (Hölldobler, 1976). Evidence has been provided, however, that recruitment rate depends on the relative time in the colony activity period. An activity period for a colony of *Pogonomyrmex* seems to consist of a sequence of standard tasks. What governs recruitment rate is the position of the colony in the sequence. The time devoted to each task may be expanded or contracted as circumstances require. Environmental factors, especially temperature, are known to affect both foraging activity and the total number of ants out of the nest (Bernstein, 1979; Whitford and Ettershank, 1975). These factors probably affect the numbers of ants performing other tasks as well. Thus, time of peak recruitment rate will vary with the colony's allocation of time to its different tasks.

Further understanding of the foraging ecology of harvester ants will require a closer look at colony behavior as well as at daily rhythms in colony activities.

Acknowledgments

The fieldwork was supported by a grant from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History. Mr. and Mrs. Finn Richards generously allowed me to use their land as a study site. I thank R. R. Snelling for identifying the ants. I am grateful to Sheri Foote for her invaluable assistance in the field, and to Bob Droual, Jim Cane, and the people at the Southwestern Research Station for their help during my stay in Arizona. I thank Peter Morin and Mark Rausher for help with statistical analysis; Peter Klopfer, Mark Rausher and Jim Cane for reviewing the manuscript; and John Gregg, Howard Topoff, and Richard Palmer for assistance with all stages of this project.

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