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The Regulation of Foraging Activity in Red Harvester Ant Colonies

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ABSTRACT: Behavioral plasticity in social insects is intriguing because colonies adjust to environmental change through the aggregated responses of individuals. Without central control, colonies adjust numbers of workers allocated to various tasks. Individual decisions are based on local information from the environment and other workers. This study examines how colonies of the seed-eating ant *Pogonomyrmex barbatus* adjust the intensity of foraging in an arid environment where conspecific neighbors compete for foraging area. The main question is how foragers decide whether to leave the nest. Patrollers search the area before foragers emerge. Removal experiments show that the return of the patrollers stimulates the onset of foraging, and later, the rate at which foragers return affects the rate at which foragers continue to leave the nest. Foraging activity is less sensitive to changes in the rate of returning foragers than to changes in the rate of returning patrollers. These results suggest that whether a colony forages at all on a given day depends on conditions detected early by patrollers but that once foraging begins, the intensity of foraging does not track, on an hourly timescale, how quickly foragers can find food.

Keywords: plasticity, task allocation, foraging.

Life requires the capacity to adjust to changing circumstances. Levins (1968) laid out the ecological and evolutionary questions this raises; in a changing environment, when does the appropriate phenotypic response to a particular condition repay the costs of producing multiple phenotypes, each for a different condition? There must be a balance between robustness, the ability to produce a reliable, consistent phenotype, and sensitivity, the ability to adjust a response to particular conditions. Most work on the evolution of phenotypic plasticity considers morphological phenotypes (e.g., Harvell 1992; Moran 1992; Sultan 2001). Behavioral plasticity or flexibility entails different behavior in different conditions (Gordon 1991*a*, 1991*b*). Studies of the evolution of behavioral plasticity include those of learning (Stephens 1991) and alternative tactics, such as a choice of mating strategies (Gross 1991; Wcislo 1997).

Behavioral plasticity in social insects is especially interesting because colonies adjust to environmental change through the aggregated responses of individuals. Social insect colonies perform various tasks, such as foraging, nest work, and brood care. As environmental conditions and colony needs change, so do the numbers of workers engaged in each task. Task allocation is the process that adjusts the numbers of workers engaged in each task in a way appropriate to the current situation. Task allocation operates without central or hierarchical control. A basic question about social insects is how individuals in the aggregate, using local information about their surroundings and each other, produce the complex behavior of colonies. How does a worker decide what to do next? The process that relates individual decisions to local information determines how quickly and how accurately a colony can change its effort when conditions change.

The evolution of phenotypic plasticity depends on the costs and benefits of a robust but possibly inappropriate response and a sensitive but possibly costly one. Such costs and benefits arise from the ecology of a particular system. Here, I consider how and when ant colonies of the red harvester ants (*Pogonomyrmex barbatus*) adjust their foraging behavior. Neighboring colonies compete for food (Gordon 1992), mostly seeds distributed heterogeneously by wind and flooding. Colonies must respond to changing foraging conditions, such as weather, food availability, and the behavior of their neighbors. The range of flexibility in foraging behavior is an important parameter in the dynamics of competition for food.

Foraging in Harvester Ants

Harvester ant patrollers search the nest mound and foraging trails before foraging begins. Foragers find food and

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bring it back to the nest. This study examines how the rate at which inactive ants leave the nest to forage depends on the rates at which patrollers, and then successful foragers, are returning to the nest.

Patrollers emerge each morning before foragers. Foragers use directions chosen earlier by the patrollers (Gordon 1991*a*) and will ignore food sources not visited earlier by patrollers (Gordon 1983).

There are two behaviorally distinct stages in patrolling each day, but experiments with marked individuals show that the same ant may perform both types of patrolling on the same day (Gordon 1991*a*). The first group of patrollers, called "nest mound patrollers," emerge from the nest for up to a few minutes and then go back inside. They stay very near the nest entrance, often waving their antennae in the air. The second group of patrollers are called "trail patrollers." The earliest trail patrollers make 5–10 min trips, moving in a zigzag pattern around the nest mound, each making frequent stops to inspect the ground with its antennae or touch antennae with other patrollers. Eventually, some trail patrollers venture around the outer edges of the mound, and then some go out on the foraging trails, making longer trips of about 20 min. The later trail patrollers eventually converge on a few foraging directions to be used that day. The last patrollers return as the foragers are beginning to emerge (Gordon 1986, 1991*a*).

Foraging activity begins as most trail patrollers are returning to the nest and continues until the end of the morning activity period. Foragers travel beyond the nest mound, then stop to search the ground for seeds, often partially buried in the soil, and each one returns directly to the nest once it finds a food item. Most foragers, >90%, stay out until they find a food item (Gordon 1991*a*). A forager can spend up to an hour searching, although the average foraging trip is about 20 min (Gordon and Kulig 1996). The trail of searching foragers forms a shape ranging from a line to a blob and, like the trails of other seed-eating ant species (Detrain et al. 2000), can extend up to about 20 m from the nest (Gordon 1995). It has been suggested that the directions of foraging trails are set by permanent chemical markers on the soil (Holldobler 1976), but the persistence of foraging direction after heavy rains and flooding wash away the soil suggests that foragers may use another method of orientation such as a sun compass.

Here, I consider how patrollers affect the intensity, rather than the direction, of foraging. There are apparently no patches that consistently offer abundant seeds for more than about a week (Gordon 1993), although the set of a colony's preferred foraging trails lasts throughout a summer's foraging season (Gordon 1995). It is not known how the patrollers influence the foragers' choices of direction. It may be that the first foragers prefer the directions in which they encounter most returning patrollers, and later foragers mimic the directions of the earlier foragers. In some ant species, both the intensity and direction of foraging are thought to be determined by chemical trails deposited by scouts and foragers (e.g., Wilson 1962). In *Pogonomyrmex barbatus*, there is no evidence that foragers normally follow recruitment trails and some evidence that, like other seed-eating species (Lopez et al. 1994; Detrain et al. 2000), they do not; in the absence of experimentally offered food, foragers of *P. barbatus* do not appear to follow exactly the same path as patrollers. Behavior apparently due to chemical trails can be induced in *P. barbatus* using artificial, very abundant baits (Holldobler 1976; Gordon 1983); in this situation, all the ants do appear to follow the same narrow, well-defined, presumably chemical path. Without artificial baits, behavior resembling experimentally induced recruitment is extremely rare, occurring only when the ants are able to subdue a large insect.

At any time, foragers and patrollers are distinct groups of individuals. Experiments with marked individuals show that ants working outside normally perform the same task, day after day, in undisturbed colonies (Gordon 1989). Ants switch tasks, but switching occurs only between certain pairs of tasks, and some transitions are irreversible. For example, a patroller may switch to foraging if extra food is available. Once an ant becomes a forager, it does not switch back to other tasks; a forager will not go back to patrolling (Gordon 1987, 1989).

An ant committed to a particular task, such as foraging, performs that task only under certain conditions and otherwise remains inactive inside the nest. For example, the number of foragers that leave the nest to forage depends on the numbers currently performing nest maintenance work (Gordon 1986, 1987) and on weather and food availability (Gordon 1991*a*).

Foragers and patrollers interact as they come in and out of the nest. When returning patrollers and returning foragers come into the nest entrance, the foragers drop their seeds, and the returning ants mix and touch antennae with inactive ants in the chamber inside the nest entrance (D. M. Gordon, personal observation). Antennae are the organs of chemical perception, and in the course of brief antennal contact, an ant perceives the cuticular hydrocarbons of another (Wagner et al. 2000). Within a *P. barbatus* colony (Wagner et al. 1998), as in other ant species (Kaib et al. 2000), cuticular hydrocarbon profiles differ according to task, apparently because tasks differ in amount of exposure to hot, dry conditions outside the nest (Wagner et al. 2001). An ant may use cuticular hydrocarbons to distinguish the task of an ant it meets. The rate of brief antennal contact influences the decision whether to perform midden work (Gordon and Mehdiabadi 1999).

Previous work suggests that interaction with returning patrollers stimulates the onset of foraging activity. First, an experimentally induced increase in numbers patrolling leads to an increase in numbers foraging (Gordon 1987). Second, the removal of patrollers for marking seemed to cause foraging to decrease or not to happen at all (Gordon 1989, 1999). Another study indicates that after foraging is well underway, interaction with returning, successful foragers stimulates further foraging. When seeds were removed from returning foragers so they went back into the nest without seeds, the overall rate of foraging decreased (Gordon 1991*a*).

The hypotheses tested here are based on the following scheme: Nest patrollers → trail patrollers → foragers ↔ foragers (with food). The return of the nest mound patrollers stimulates the activity of the trail patrollers; the return of the trail patrollers stimulates the onset of foraging; and once foraging has begun, the return of successful foragers stimulates further foraging. I tested whether removing the nest mound patrollers decreases the activity of trail patrollers, whether removing trail patrollers inhibits the onset of foraging activity, and whether removing foragers returning with food decreases foraging activity.

Methods

The study was performed in July and August 2000 at a site near Rodeo, New Mexico. This population of about 300 *Pogonomyrmex barbatus* colonies has been studied since 1985 (Gordon 1999), and the ages of the colonies are known from an annual census (details of census methods in Gordon and Kulig 1996). Each colony is given an identification number, and these are the numbers used to identify the colonies discussed here.

Outside the nest, ants of *P. barbatus* perform various tasks. Midden workers sort and pile the refuse pile or midden. Nest maintenance workers build and repair chambers and tunnels inside the nest, and they emerge outside to carry out dry soil and debris. Patrolling and foraging are described above.

There were five treatments (table 1). The first was undisturbed ($n = 5$ colony days). No ants were removed. In the second treatment, one in five returning ants were removed ($n = 6$ colony days). The observer collected every fifth ant returning to the nest. We did not attempt to identify the task of the ants removed but did attempt to avoid collecting ants of tasks other than patrolling. To avoid collecting foragers, ants were not collected if they were obviously carrying something; for returning ants, these would most likely be foragers. To avoid collecting nest maintenance workers or midden workers, ants were not collected if they were returning from the midden, which is where midden workers tend to be and is the location to which nest maintenance workers carry refuse. Although some of the ants collected may have been returning foragers carrying a seed too small to see, probably many of them were nest mound and trail patrollers. In the third treatment, nest mound patrollers were removed ($n = 3$ colony days). All ants behaving like nest mound patrollers were collected within 5 cm of the nest entrance at the beginning of the morning activity period, before ants of other tasks had emerged. In the fourth treatment, trail patrollers were removed ($n = 5$ colony days). All ants behaving like trail patrollers were collected as they returned to the nest. In the fifth treatment, returning foragers with seeds were removed ($n = 4$ colony days). All foragers with seeds were collected as they returned to the nest. In all removal experiments, ants collected were kept in a plastic box with access to water for up to 1 h after all colony activity stopped and then allowed to return to the nest.

Table 1: Colonies used in each treatment

Treatment	615	685	839	872	558	816	855
Undisturbed	X	X	X	X			
Removed:							
One in five returning	X		X	X	X	X	X
Nest mound patroller	X	X		X			
Trail patrollers	X	X	X	X			X
Foragers	X	X	X	X			

Note: Numbers are colony identification numbers. Each colony was observed on 1 d in the indicated condition, except that colony 685 was observed on 2 d when undisturbed.

Table 1 shows which colonies were used in each treatment. Colony ages (by colony number) were 8 (558), 6 (615), 5 (685), 3 (816), 3 (839), 2 (855), and 2 (872) yr. Colonies ages 2–3 yr have about 4,000 ants; colonies 5 yr and older have about 10,000 ants, but a larger proportion of ants in the small, young colony work outside the nest (Gordon 1992). Each colony was observed when undisturbed on a different day from July 31 to August 10; colony 685 was observed twice when undisturbed, on August 2 and 10. One in five returning ants were removed on July 26 and 28. Nest mound patroller removal, trail patroller removal, and forager removal were performed on different days from August 1 to 12.

Counting was done by two or three observers who watched the nest entrance and counted ant numbers using a click counter. Observers avoided sitting, standing, or casting a shadow in foraging directions or otherwise disturbing the ants. Observer 1 recorded the numbers of ants leaving the nest. Observer 2 recorded both numbers of

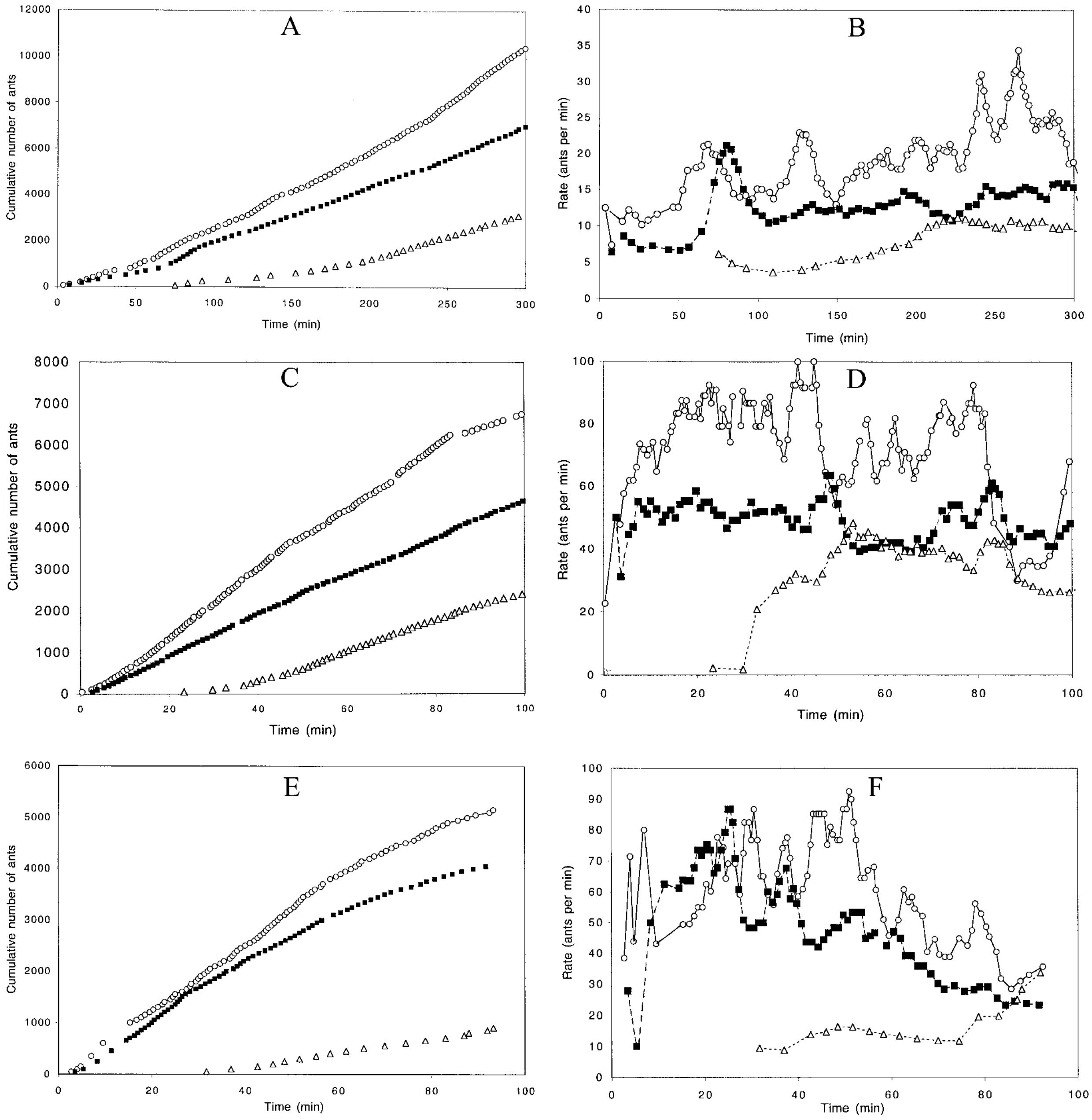

Figure 1: Each pair of graphs shows cumulative number of ants (*A*, *C*, *E*) and rate (*B*, *D*, *F*) in ants per minute for one undisturbed colony on the same day. Rates shown are the moving averages of rate over five time intervals. Open circles show ants leaving the nest, filled squares show ants returning to the nest without seeds, and open triangles show ants returning to the nest with seeds. *A*, *B*, Colony 685, August 10; *C*, *D*, Colony 615, August 3; *E*, *F*, Colony 872, July 31.

ants returning to the nest with nothing in their mandibles and numbers of ants returning to the nest with seeds. Ants of the latter category are returning foragers. An ant returning to the nest carrying something in its mandibles is definitely a forager, but counts of ants returning with seeds (latter category) may underestimate numbers of foragers because some food items are too small for an observer to see easily. In some cases, all three of these counts (leaving the nest, returning without seeds, and returning with seeds) could be made by one observer. Another observer stood nearby with a stopwatch, looking at the counters, and wrote down the time at which each count increased by another 50 ants. An observer also counted occasionally the rate of nest maintenance workers leaving the nest as the numbers, out of 10, of ants leaving the nest that were carrying something and recorded the times at which these counts were made.

These counts were used to plot cumulative number of ants leaving and returning to the nest as a function of time and to calculate rates in ants per min. All rates higher than 100 ants per minute were changed to 100 because observers could not accurately press the key on a counter faster than 100 times per minute. Rates as high as 100 ants per min occurred only in ants leaving the nest.

The study was done during a period of hot, dry weather. There is a characteristic sequence of activities each morning, beginning at sunrise and ending at midday (Gordon 1984). Activity outside the nest is limited by high temperatures (Whitford and Ettershank 1975), and on hot days, the daily sequence of tasks is performed more rapidly and activity ends sooner. At the peak of foraging activity, only foragers are active (Gordon 1984). In this study, we continued observations of the onset of foraging in a colony until other nearby colonies had well-established streams of foragers. On hot days, it took undisturbed colonies about 65–100 min to reach the time when the rate of outgoing foragers was at its peak and the rate at which foragers returned with seeds seemed to be steady. On hot days, the morning activity period lasted only until about 8:30 or 9:00 A.M., not more than about 180 min after the colony emerged. However, on a cool overcast day, such as August 10, when the second observation was made of colony 685 when undisturbed (fig. 1*A*), the activity period was longer, lasting well past the 300 min during which we observed the colony.

Results

Undisturbed Colonies

In undisturbed colonies, the rate at which ants emerged from the nest increased rapidly over the first 20–30 min of observation. The rate at which ants returned without seeds was steadier and lower. After a lag, which ranged from 15 to 75 min in the five observations of undisturbed colonies, ants began to return with seeds. Figure 1 shows the results from observations of three colonies when undisturbed. Counts are shown both as cumulative numbers of ants and as rates. The other two observations of undisturbed colonies, not shown, had similar results.

Removals

Nest Mound Patrollers Removed. When nest mound patrollers were removed, foraging activity was inhibited in all three trials. In colony 872, 42 patrollers were collected in 2 h, in colony 685, three were collected in 75 min, and in colony 615, 45 were collected in 2 h. While returning nest mound patrollers were being removed, nest mound patrollers left the nest in spurts; a few patrollers were collected, activity ceased, then a few more came out and were collected, and so on. In two out of the three trials, activity ceased altogether for at least 60 min. In the other trial with colony 615, nest patrollers continued to emerge and were collected, one or two at a time, for 125 min. In all three trials, after at least 1 h with no foraging activity, newly emerged nest patrollers were allowed to return to the nest, and foraging activity eventually resumed.

Trail Patrollers Removed. When trail patrollers were removed, foraging activity was inhibited. Results are shown for colony 872 (fig. 2; one of the colonies shown as undisturbed in fig. 1), in which 43 trail patrollers were collected in 89 min, and no ants left the nest for >1 h. In colony 839, 83 patrollers were removed in 15 min, and no ants left the nest for >100 min. In colony 615, 116 were collected in 120 min, and no ants left the nest for >1 h. In colony 855, 16 ants were collected in 39 min, and all activity ceased for >1 h. In colony 685, however, 300 patrollers were collected in 85 min, and while activity seemed to slow slightly, foraging continued.

In the four removals of trail patrollers when colony activity slowed, all ants returned to the nest within about 20 min after the first group of trail patrollers were collected. During this time, ants returning with seeds were allowed to go back into the nest. These might have been trail patrollers, who sometimes return with seeds, but they were allowed to return because they might instead have been early foragers. Nest maintenance workers, who emerged from the nest carrying a bit of soil, were allowed to return to the nest after they deposited their load. However, very few nest maintenance workers emerged during patroller removals. Once activity slowed, there were repeated attempts to resume activity, during which one or more patrollers emerged and were collected as they returned to the nest. The mean intervals between subsequent attempts ranged from 7.4 to 18.5 min, and the numbers of attempts ranged from four to nine, after which none of the colonies attempted to emerge again for at least 1 h.

One in Five Returning Removed. When one in every five returning ants were removed, foraging activity continued. In four colonies, 100 ants were removed during the time it took 500 ants to return, which ranged from 14 to 60 min. In another two colonies, 200 ants were removed during the time it took 1,000 ants to return, which ranged from 60 to 80 min. Ants continued to leave the nest in

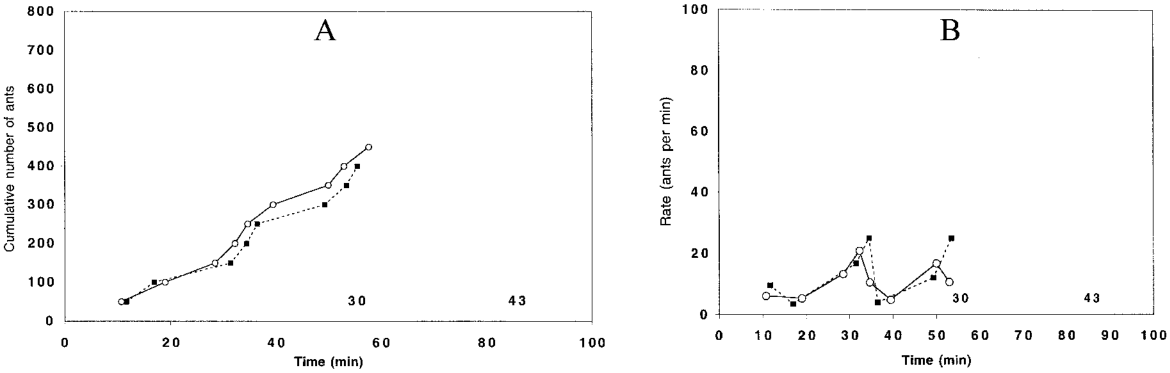

Figure 2: Trail patrollers removed in colony 872 on August 2. *A*, Cumulative number of ants. *B*, Rate in ants per minute as in figure 1. Open circles show ants leaving the nest, filled squares show ants returning to the nest without seeds, and open triangles show ants returning to the nest with seeds. Numbers above the *X*-axis indicate the time at which that number of returning trail patrollers were removed.

all six colonies, and all colonies foraged actively on the day of removals.

Foragers Removed. When foragers returning to the nest with seeds were removed, foraging activity diminished somewhat in three out of four trials. In colonies 615, 872, and 685, foraging slowed down after 71–200 foragers were collected. Results are shown in figure 3 for colony 615, one of the colonies shown when undisturbed in figure 1. The decrease in the rate of foraging activity always occurred about 1 h after the first 50–100 ants were collected. For example, in figure 3, there is a plateau in numbers leaving the nest beginning at about 130 min, about 1 h after the first 50 returning foragers were collected at 70 min. The typical delay of about 60 min, in response to the absence of returning foragers, was much longer than the time it would have taken the foragers to return. The average duration of a foraging trip is 23 min (Gordon and Kulig 1996); in 59 observations of individual foragers in nine other colonies in the summer of 2000, we found that the average duration of foraging trips ranged from 7.2 min (SD = 3.1) in one colony to 26.8 min (SD = 20.7) in another (F. R. Adler and D. M. Gordon, unpublished data).

The removal of returning foragers did not usually stop foraging activity. In two out of the three trials in which foraging activity decreased, in colonies 615 (fig. 3) and 872, foraging resumed again after 70 and 90 min, respectively, although we continued to collect returning foragers. In the third trial, with colony 685, foraging stopped and did not resume. In the fourth trial, with colony 839, the removal of 313 returning foragers had no apparent effect on foraging activity, which was so high that we were unable to remove more than about half the returning foragers.

Comparison of Removal Treatments

The removal of patrollers or foragers decreased the rate of foraging. I compared the average rate of foragers returning with seeds in the following treatments: undisturbed, trail patrollers removed, and foragers removed. I omitted nest mound patroller removals from this analysis because the effect was obvious without statistical tests; the rate of return with seeds was either zero or very close to it in all removals of nest mound patrollers. The average rate of foragers returning with seeds was calculated for a given colony on a given day as the total number of ants that returned with seeds that day, divided by the total time the colony was observed that day. For forager removal experiments, I included the number of returning foragers we collected in the total number of ants returning with seeds. Average rates were significantly different among treatments (ANOVA: $F = 9.4$, $\mathrm{df} = 2, 11$, $P < .004$, $SS = 782.1$; fig. 4). The average rate of ants returning with seeds per min when foragers were removed and when trail patrollers were removed were each significantly different from the rate in undisturbed colonies, but the two removal treatments were not significantly different from each other (Fisher's protected least significant difference test: $P < .05$). A similar analysis was performed using the average rate of ants returning to the nest (with and without seeds summed), including as a fourth treatment the removal of one in five returning ants. Again, rates of return to the nest were lower in the removal treatments than in undisturbed colonies and differed significantly among treatments ($F = 10.5$, $\mathrm{df} = 3, 17$, $P < .0004$, $SS = 7{,}812.5$).

The effect on overall activity, per ant removed, of removing a patroller seems to be greater than the effect of removing a returning forager. Figure 5 shows average rates of ants returning to the nest in four treatments: undis-

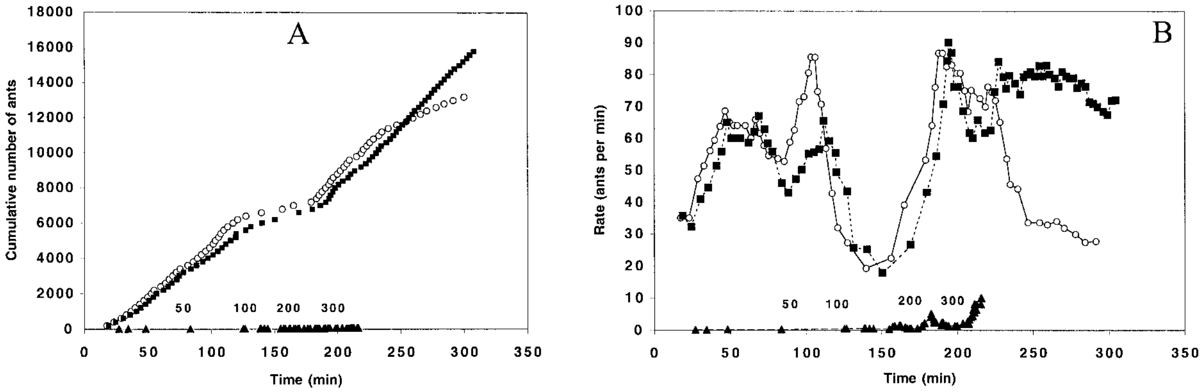

Figure 3: Foragers returning with seeds removed in colony 615 on August 10. *A*, Cumulative number of ants. *B*, Rate in ants per minute as in figure 1. Open circles show ants leaving the nest, filled squares show ants returning to the nest without seeds, and filled triangles show ants returning to the nest with seeds that were missed when collecting all returning foragers. Numbers above the *X*-axis indicate the time at which that number of returning foragers were removed.

turbed, trail patrollers removed, one in five ants removed, and foragers removed. These rates are a measure of overall activity. The *X*-axis shows numbers removed, with zero removed in undisturbed colonies. Many more foragers than patrollers were removed, but the removal of patrollers inhibited activity more. The activity rates for forager removals were close to those of undisturbed colonies, while the rates were much lower for removal of one in five ants (probably mostly patrollers) and for removal of patrollers. Thus, the removal of few patrollers had a greater effect than the removal of many foragers.

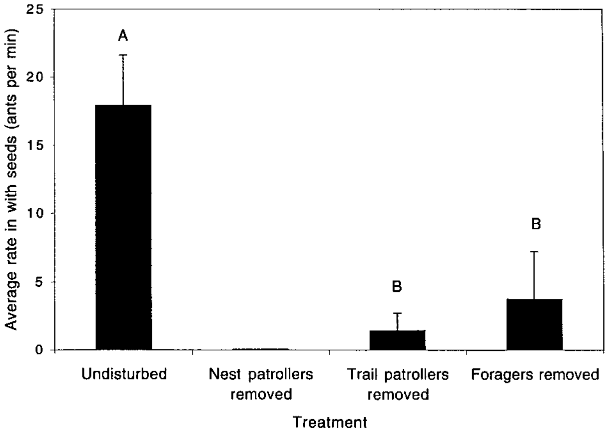

Figure 4: Average rate of ants returning with seeds (ants per min). Error bars show SE of the mean. The average rate for nest patroller removals was 0.01 with SE = 0.01. Different letters indicate the means were significantly different; Fisher's protected least significant difference test: $P < .05$.

Discussion

The results of removal experiments are consistent with the hypothesis that returning patrollers and returning foragers influence the rate at which inactive foragers leave the nest to forage. When nest patrollers do not return, activity outside the nest ceases; there is no further patrolling, and foraging never begins. When trail patrollers do not return, outside activity ceases, and foraging never begins. When foragers with seeds do not return, there is a decrease in activity, but later, foraging activity often resumes.

Different pressures may favor either consistently high foraging or the ability to adjust foraging to food availability. Behavioral studies show that colonies compete with their conspecific neighbors for foraging areas (Gordon 1991*a*, 1992). Ecological studies show that crowding influences the probability of successful founding (Gordon and Kulig 1996) and the production of reproductives in some years (Gordon and Wagner 1997; Wagner and Gordon 1999) and has a slight effect on mortality (Gordon and Kulig 1998). In an environment in which resources are limiting and ephemeral, consistently high foraging effort may put a colony at an advantage, relative to its neighbors.

It appears that the patrollers influence an all-or-none decision, whether to forage or not on a given day. The two groups of patrollers, nest mound and trail, may have different roles. The return of the first nest mound patrollers seems to inform the colony that it is feasible to leave the nest that day. *Pogonomyrmex* harvester ants obtain most of their water from metabolizing the fats in seeds (MacKay 1985), yet they lose water while foraging when the air is hot and dry. Thus, it may be worthwhile for a

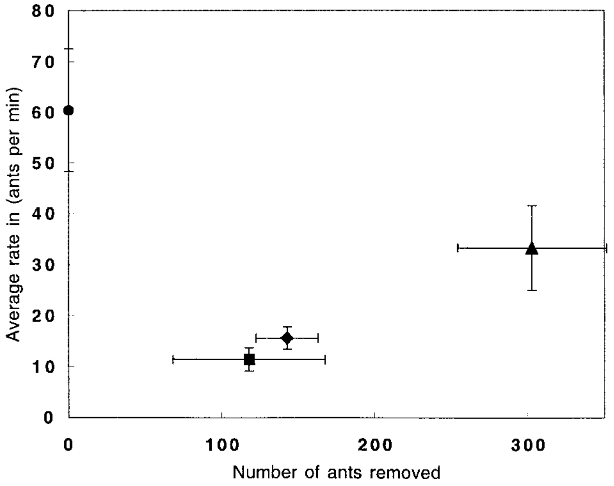

Figure 5: Average rate of ants entering the nest as a function of number removed. Average rates were calculated as total numbers returning divided by total time. The circle shows the average for undisturbed trials, the diamond shows the average for removals of one in five returning ants removed, the square shows the average for trail patroller removals, and the triangle shows the average for removals of returning foragers.

colony to rely on stored food when foraging costs are high. Nest mound patrollers may assess humidity and temperature. I do not know what, other than a person with an aspirator, might cause all of the patrollers to disappear completely. I once saw some ants blown off the nest mound by a strong wind. Heavy flooding, which carries soil, would also carry ants. Since there is no evidence that ants inside the nest await the return of particular individuals, the complete disappearance of ants in my experiments may be no different from other more ordinary events that cause a delay in the ants' return. After the nest mound patrollers have gone back in, trail patrollers choose foraging directions. Their choice may depend on food availability. Also, trail patrollers meet the patrollers of neighboring colonies (D. M. Gordon, personal observation), and this may be how a colony's choice of foraging direction is influenced by the foraging directions of its neighbors (Gordon 1992; Gordon and Kulig 1996).

Patroller removal seems to have a greater effect than forager removal in two ways. First, patroller removal sometimes shut down colonies completely, while forager removal never did. This suggests that the return of patrollers is essential to initiate foraging. Second, the effect, per ant removed, of removing a patroller is greater than that of removing a forager; more foragers than patrollers had to be removed to diminish foraging rate by a given amount (fig. 5). The number of patrollers active at any time is usually at least an order of magnitude smaller than the number of foragers active (e.g., 50 patrollers and 1,000 foragers would not be unusual in a mature colony; Gordon 1983; Gordon and Kulig 1996). Thus, each returning patroller may make a larger relative contribution to the rate of interaction with inactive foragers than does each returning forager.

The onset of foraging seems to be more sensitive to disturbance than the continuation of foraging once it has begun. When returning foragers were removed, it took about twice the usual duration of foraging trips for foraging activity to decrease. This suggests that once foraging activity is in progress, a forager's decision whether to leave the nest is not much affected by the return of successful foragers. The rate at which successful foragers return is correlated with food availability; when food is abundant, foragers find food more rapidly. Since most seeds collected by *Pogonomyrmex barbatus* at this site are distributed by wind and flooding (Gordon 1993), the food available to foragers may not differ much from that encountered by the trail patrollers some hours earlier. Perhaps there is a threshold, in numbers or rate of returned patrollers, that is required for foraging to begin, and once begun, feedback on foraging success has only a small effect. This effect, though small, is real; eventually, when the rate of return decreases, there is some adjustment of foraging activity, and the rate at which ants leave the nest also decreases. This is consistent with the previous result that removing the food carried by returning foragers decreased the overall rate of foraging (Gordon 1991*a*).

The negative effect of removals on subsequent activity is not simply due to the absence of the ants that otherwise would have left the nest. There are four lines of evidence for this. First, removal of a given number of ants has different effects, depending on the task of the ants removed (fig. 5). The removal of a small number of patrollers generally has a greater effect than the removal of larger numbers of other ants. For example, when 400 returning foragers were removed from colony 872, foraging slowed but then resumed. However, when only 43 patrollers were removed from the same colony, activity ceased. Second, in the patroller removals, activity stopped although the numbers removed were much smaller than the numbers of patrollers or foragers that emerged when the same colonies were undisturbed. For example, in 872 when undisturbed, ants often left the nest at rates higher than 50 ants per min (fig. 1*F*), yet activity ceased when 43 patrollers were removed. Third, when foragers were removed, ants stopped leaving the nest in two colonies but were able to resume high rates of foraging activity before the collected ants were returned (e.g., fig. 3). Fourth, colonies responded similarly despite differences in colony age. Since older colonies are much larger, this suggests that numbers of available ants did not determine the response to removals.

A comparison of total numbers of ants coming in and going out suggests that our counts were reasonably accurate. In five observations of undisturbed colonies, and in three out of four observations when patrollers were removed, the total numbers of ants coming in and going out were similar, within 6% of the numbers of ants going out. This corresponds to a reasonable number of ants that had not yet returned to the nest when observations ended. However, when foragers were removed, the numbers of ants coming in were much larger than numbers of ants going out, from 12% to 20% of the numbers of ants going out. Perhaps many extra patrollers left the nest in response to forager removals.

It appears that a forager uses the rate at which it encounters certain types of returning workers in deciding whether to leave the nest itself. In other social insects, the interval elapsed between interactions affects foraging decisions (Jeanne 1999; O'Donnell 2001). This interpretation assumes that the rate at which an ant inside the nest encounters ants of a certain type, which we did not measure, is a function of the rate at which that type of ants enter the nest, which we did measure. The relation between individual encounter rate and the rate at which ants enter the nest depends on how ants mix in the chamber just inside the nest entrance. This relation might not be linear, for example, if a change in the rate at which ants come in leads to a change in the way they mix. Observations of marked ants inside the nest entrance with a fiber optics microscope suggest random mixing of ants inside the nest entrance, but further work is needed to determine this.

The results suggest that returning foragers contribute to the success or persistence of the foragers that are currently leaving the nest. When the returning foragers were removed, there were unusually high numbers of ants that returned without seeds. For example, when colony 615 was undisturbed, cumulative numbers of ants returning without seeds were well below numbers of ants going out (fig. 1*C*); in the same colony when foragers were removed, numbers returning without seeds were about the same as numbers going out (fig. 3*A*). Moreover, the rate of return with seeds was uncharacteristically low. For example, when colony 615 was undisturbed, 300 ants came in with seeds 16 min after the first 50 ants. When returning foragers were removed in colony 615, it took about 3 h for 300 ants to return with seeds after the first 50 were collected. This suggests that an outgoing forager is less likely to return with a seed when no foragers are returning to the nest with seeds. Removals were not likely to affect interactions in the foraging area far from the nest since returning foragers were removed within 1 m of the nest entrance, after they found a seed and came most of the way back to the nest. Perhaps outgoing foragers learn something at or near the nest entrance from the returning foragers, such as the odor of the seeds that are available that day, or perhaps the rate of incoming foragers influences how long an outgoing forager persists in searching. Further work is needed to distinguish the effect of foragers from that of their seeds; the ideal experiment would involve returning seeds without foragers.

Colonies differ in how much they forage, and these colony-specific trends persist from year to year (Gordon 1991*a*). Colonies may vary in the ways that inactive foragers respond to interaction with patrollers. For example, in one colony, low numbers of interactions with patrollers may be sufficient to elicit foraging activity, and in such a colony, foraging would often be high. In another colony, high numbers of interactions with returning foragers might be needed to sustain foraging once it has begun, and in such a colony, foraging intensity might be more sensitive to food availability. Other work is underway to test how variation among colonies in foraging behavior is related to variation in reproductive success. This may help us to understand how *P. barbatus* colonies balance robustness, which leads a colony to send out many foragers no matter what, and sensitivity, which allows a colony to adjust its foraging according to food availability and environmental conditions.

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