Anim. Behav., 1986, **34**, 1402–1419

The dynamics of the daily round of the harvester ant colony (*Pogonomyrmex barbatus*)

DEBORAH M. GORDON
Museum of Comparative Zoology and Society of Fellows, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

Abstract. Colonies of the red harvester ant, *Pogonomyrmex barbatus*, do various tasks outside the nest. There is a daily temporal pattern in the numbers of ants engaged in each of five activities: foraging, nest maintenance, patrolling, midden work and convening. Perturbations were carried out in the field to investigate how the daily round changes in response to environmental events and colony needs. Interfering with nest maintenance, foraging or both caused changes in the temporal patterns in all five of the observed activities. Removing nest maintenance workers, foragers or both caused the numbers involved in all five activities to decrease, and there were temporal patterns in the effects of removals. The results of both interference and removal experiments show that the extent to which a worker group does one activity affects the behaviour of other groups. When nest maintenance or foraging is impeded experimentally, these two activities are of reciprocal priority. When both are impeded, foraging is of higher priority than nest maintenance.

Harvester ants forage, patrol, maintain the nest area and foraging trails, collect and arrange pebbles on the nest, and gather in small groups, inspecting and grooming each other. The behaviour of the colony outside the nest at any moment can be described by citing the number of ants engaged in each of the five activities. The numbers change throughout the day in a predictable manner. There is a daily temporal pattern in the numbers of ants engaged in each activity. Describing the pattern in all activities is describing the daily round of the colony.

Daily rounds are colony-specific (Gordon 1983a) and species-specific (Gordon 1984a), and response to experimental manipulations may depend on the stage in the daily round when experiments are done (e.g. Gordon 1983b). Thus, the daily round of a harvester ant colony provides a baseline from which to investigate colony behaviour. Certain aspects of chemical communication, response to new food sources and territorial behaviour can be explained in the context of the daily round (Gordon 1983b,c, 1984b).

It would be a mistake, however, to think of the daily round as a rigid programme. Temporal patterns in the numbers of ants engaged in each activity can change. On some days, for example, foraging predominates; on others, colonies do mainly nest maintenance work (personal observation). The concept of the daily round is, loosely speaking, that of an equilibrium state, but the dynamics of colony organization are not yet understood. What events will alter the daily round, by how much, and for how long? Is there more than one equilibrium state?

This study begins an exploration of the dynamics relating colony priorities and external events. I perturbed the daily rounds of harvester ant colonies and examined the resulting changes in daily rounds. I did two kinds of perturbation experiments: first, interfering with nest maintenance, foraging, or both; and second, removing nest maintenance workers, foragers or both. In the interference experiments, nest maintenance workers were presented with a pile of toothpicks that had to be cleared away before other activities could be done and barriers were placed across the foraging trails to prevent foragers from going directly to their destination. In the removal experiments, workers engaged in each task were removed from the colony.

The following questions were considered.

(1) How independent are different worker groups? First, do changes in the temporal pattern of one activity affect temporal patterns in other activities? Little is known about the dynamics of the temporal relationships between the different tasks of an ant colony. By interfering with nest maintenance and foraging, I changed the temporal pattern in each of these two activities. Subsequent

temporal patterns in other activities were then examined. Second, does the removal of ants doing nest maintenance and/or foraging affect the numbers of workers, and temporal patterns, in other activities? Individual ants are known to switch tasks in response to environmental disturbances (Meudec & Lenoir 1982) and the removal of workers (Wilson 1983, 1984). Here I consider how, at the group level, a decrease in the numbers available to do one task affects the numbers and temporal patterns in other tasks.

(2) Which aspects of the daily round are flexible? First, are nest maintenance and foraging of equal priority? Common sense suggests that foraging is of a high priority to an ant colony. However, harvester ant colonies store seeds inside the nest (MacKay 1981) and are able to survive periods of inactivity (Whitford & Ettershank 1975). Nest maintenance workers clear and maintain the foraging trails and nest mounds, which are thought to be the site of colony-specific pheromones used in territorial behaviour (Holldobler 1976). Thus nest maintenance may be crucial in interspecific and inter-colony relationships, as well as in keeping the nest mound clear for other activities, and is conceivably as important to the colony, in the short term, as foraging.

If foraging and nest maintenance are of equal priority, then perturbing each activity singly would have similar effects, and perturbing both would have the same effect, but of larger magnitude.

Second, which aspects of the daily round are preserved despite perturbations? Patrolling precedes foraging in the daily round of undisturbed colonies, and it appears that patrollers recruit foragers to new food sources (Gordon 1983b). If the temporal pattern in foraging is changed, will patrolling still precede it? I examined which temporal relationships between activities persist after perturbations.

The methods used in this study reflect a concern with patterns in group, rather than individual, behaviour. The daily round is an example of such a pattern. In exploring whether and how temporal patterns in different activities are related to each other, this study has two goals. The first is to examine the relationship between colony priorities and external events in a harvester ant colony. The second is to offer some tractable questions about group behaviour that may be useful in investigating the organization of other animal societies.

INTERFERENCE EXPERIMENTS

Methods

The study was conducted in a chapparal-mesquite habitat in the Lower Sonoran desert near Rodeo, New Mexico, during a stay at the Southwestern Research Station. Twelve colonies of the harvester ant *Pogonomyrmex barbatus* were observed during six observation periods from 19 July to 30 August 1984. All observation periods (OP) were 6 days long, except for OP5, which was only 3 days long. Each colony was observed once each hour from 0600 until 1300 hours. All activities seen outside the nest were classified into the five activity types listed above and in Table I. An observation consisted of recording the numbers of ants engaged in each activity within 1.3 m of the nest entrance. This area contains workers in all five activities, including some of the foragers, but only about the first 0.3 m of the foraging trail. The sum of the workers engaged in the five activities represents the total number of ants outside the nest.

Experiments were conducted during OP2, OP4, and OP6. Six of the 12 colonies were left undisturbed as controls. The other six were divided into three groups of two colonies each. In one group, a pile of toothpicks was placed near the nest entrance after the 0700 hours and before the 0900 hours observations, when at least nine maintenance workers had been seen at work on the nest mound. The number of toothpicks was increased as follows: OP2, 100 toothpicks; OP4, 200 toothpicks; OP6, 300 toothpicks. The ants usually moved all the toothpicks to the perimeter of the nest mound within 1 h. Once there, the toothpicks were no longer manipulated by the ants. I removed all the toothpicks at the end of each day.

In the second group of two colonies, plastic rectangular barriers (15 × 10 cm) with two V-shaped indentations (4 cm long) cut, wide end down, into the bottom of each rectangle, were placed across foraging trails. Each rectangle was bent to a 90° angle lengthwise, across the bases of the Vs, and held on the ground with rocks. Ants approaching from one side encountered the wide end of the V and passed through the barrier easily. From the other side, they encountered only a small opening, formed by the base of the V. The presence of the barrier caused interference on the foraging trail, as the ants went either back and forth along it until getting through an opening, or around the

Table I. Classification of colony activities

Activity	Behaviour
Foraging	Ants travel directly away from the nest entrance, not carrying anything, on foraging trail
	Ants travel directly to the nest entrance, usually carrying a seed or insect bit, on foraging trail
Nest maintenance	Carrying out: ants come out of the nest entrance carrying something, put it down in the nest yard, and go back into the nest
	Clearing vegetation: ants climb in vegetation at edge of nest yard, clip pieces of it off with mandibles
	Ants rearrange sand particles near nest entrance, removing obstructions to the path of ants entering and leaving the nest
Patrolling	Ant walks with frequent stops and changes in direction (compared to foragers). Abdomen is often bent underneath the thorax. Objects and other ants encountered are frequently inspected with antennae.
	At the site of a disturbance, such as a new object in the nest yard not brought in by ants, ants gather and stand with mandibles open
Midden work	Ants stand on the midden, repiling it or inspecting it with antennae
	Ants move objects from one midden to another midden in nest yard
	Ants come into the nest yard, not along the foraging trail, bringing small pebbles, and put them down on the nest mound
Convening	Ants mill around the nest entrance. Frequent antennal contacts between workers

barrier. The number of barriers was increased as follows: OP2, two barriers on one trail; OP4 and OP6, four barriers on two trails (the number of barriers was not increased in OP6 since most colonies had only two major trunk trails). Barriers were placed 1·5 m and 1·8 m from the nest entrance, outside the 1·3 m radius of observation, and oriented so that ants going in either direction along the trail would encounter the wide and narrow openings once each. Barriers were put down after the 0800 hours observation and before the 0900 hours one, when at least 20 foragers had been observed on the trail, and were removed at the end of each day.

The third experimental group received both toothpicks and barriers. The timing and magnitude of each perturbation were identical with those described above.

A total of 2682 observations were made.

For each colony, all of the observations were converted to proportions of the largest total number of ants ever observed outside the nest in that colony. This was done to normalize for differences in colony sizes. The proportions were submitted to an arcsin transformation.

Data from the non-experimental observation periods (OP1, OP3 and OP5) were analysed separately from the data for the experimental ones (OP2, OP4 and OP6). Observations from the experimental periods were used in a four-way full-factorial ANOVA (BMDP 1981, P4V) with treatment (undisturbed, toothpicks, barriers or both), OP, activity and hour as main effects. Three a priori contrasts were made by doing three separate four-way ANOVAs comparing each experimental treatment with the undisturbed colonies. Thus the undisturbed colonies in the same observation period were used as controls.

To test whether experimental and undisturbed colonies were alike before the experiments, a similar ANOVA was done on the data from OP1 (a three-way ANOVA since there was no OP effect). To test for residual effects of the experiments, similar ANOVAs were done using the data from OP3 and OP5, when no perturbations were done (a four-way ANOVA as described above with treatment, OP, activity and hour as main effects).

Computer graphics (Fig. 1) were done on an Apollo DN300 using PRIMH under ISP under AEGIS.

Results

Perturbations affected not only the activities that were interfered with, but other activities as well by causing changes in activity rhythms. The daily patterns in colony activities in response to each treatment are shown in Fig. 1. The figure looks complex but is intended to convey a simple point: when one activity was perturbed, activity rhythms in other activities changed as well. The figure does not uniquely represent what these changes were, or make it possible to assess visually their statistical significance, which is discussed below with the ANOVA results.

Each of the smaller figures in Fig. 1 represents the behaviour of one treatment group in each of the three observation periods in which experiments were done (OP2, OP4 and OP6). The figures are projections of three-dimensional curves. The data

Table II. Interference experiments: results of ANOVA comparing treatment groups (including controls) before experiments began (OP1)

	Type 1			
Effect	*df*	Sum of squares	*F*	*P*
Activity	4	33·97	1247·9	0·0001
Hour	5	5·35	157·3	0·0001
Treatment	3	0·05	2·5	0·0577*
Activity × hour	20	11·23	82·5	0·0001
Activity × treatment	12	0·23	2·8	0·0010
Hour × treatment	15	0·17	1·6	0·0606
Activity × hour × treatment	60	0·35	0·9	0·7706
Error	2025	13·78		

* See footnote to Table VIII.

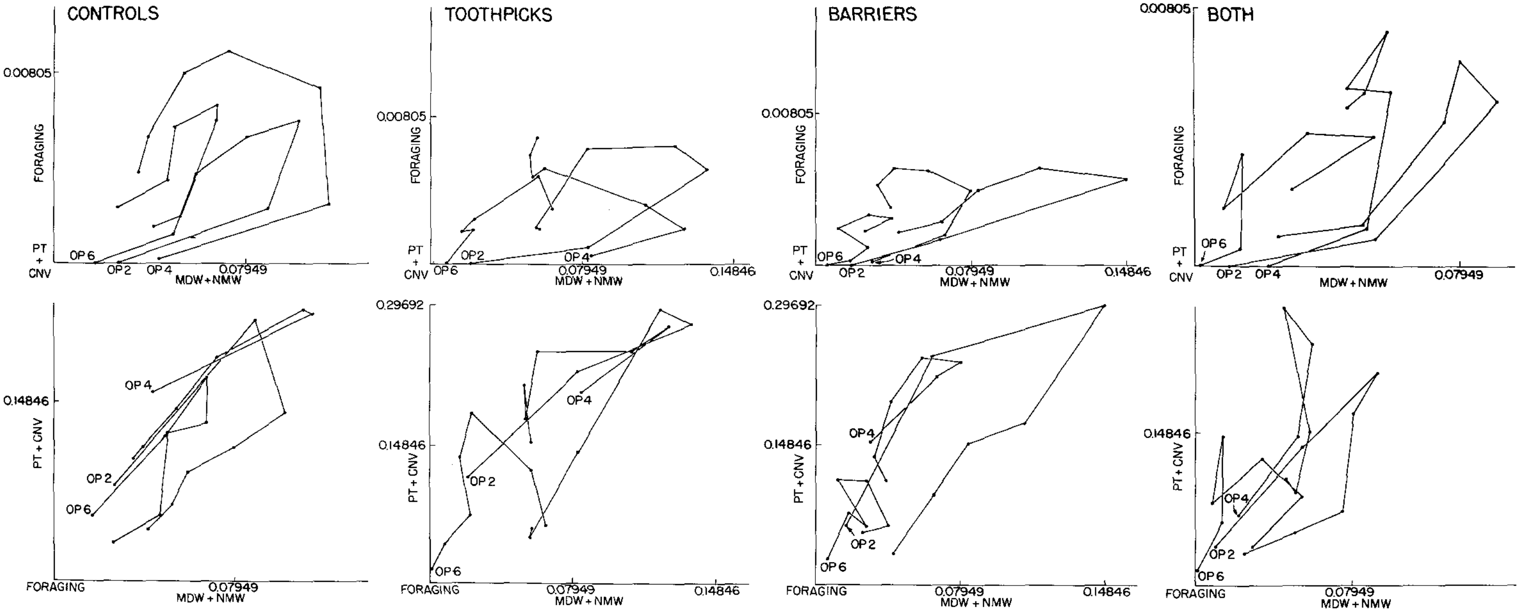

Figure 1. Interference experiments: temporal patterns in the behaviour of all treatment groups (see text for explanation). Axes represent mean normalized numbers of ants doing (1) foraging, (2) midden work + nest maintenance (axis is labelled MDW + NMW) and (3) patrolling + convening (axis is labelled PT + CNV). The third axis, labelled at the vertex of the other two, points into the plane of the paper. Each point shows the data for one hour, from 0600–0700 hours through 1200–1300 hours. The first point in each trajectory, showing the data for 0600–0700 hours, is labelled with the OP number (OP2, OP4 or OP6).

for each treatment group are shown in two different projections. Each point represents the mean normalized numbers in all five activities, in a particular hour. Each line is a trajectory connecting the data for each of the 7 h that colonies were observed. Each trajectory represents the daily temporal pattern in colony activities for one observation period and treatment group.

The effect of the interference perturbations on activities that were not perturbed can be visually assessed, by comparing the trajectory for the control colonies in a given OP with the trajectory for each experimental group in the same OP. If a perturbation had caused a change in only one activity, the trajectory for the experimental group would be shifted up or down one axis, but would have a shape similar to that of the control group's trajectory. The radical differences in overall shape, seen when comparing each treatment with the control in the same OP, are due to differences in temporal patterns in more than one activity.

For example, in the upper row of figures, compare the trajectory for OP4 in the controls with that for OP4 in the 'barriers' group. The trajectory for the barriers treatment is not as high, due to a reduction in foraging, but it is also of a different shape, especially later in the day, due to changes in other activities. In the lower row of figures, the two analogous trajectories are also of markedly different shape.

Before the experiments began, colonies in different prospective treatment groups did not differ significantly in the mean normalized numbers of workers engaged in each activity (no significant treatment effect, Table II), or show different activity rhythms (no significant treatment × activity × hour interactions).

As the summer progressed, changes in the weather such as lower temperature and unusually heavy rainfall, caused significant differences among observation periods in the control colonies (Table III; Fig. 1). Harvester ant colonies devote different proportions of the outside work force to each activity, and in each activity the proportions depend on the time of day (Gordon 1984a). This led to significant effects involving the activity and time of day in all of the observation periods.

Table IV shows the results of the ANOVA for experimental observation periods. Of most interest is the significant interaction of treatment × activity × hour; daily activity rhythms differed among the treatments. Figure 2 shows these interactions. Each point represents the value of the treatment × activity × hour mean after the lower-order effects (i.e. overall mean, treatment, activity, hour and all two-way effects) have been subtracted out (Brooks 1985) (see Appendix). Thus the figure shows the effect of treatment on activity rhythms after main effects and lower-order interactions have been taken into account. Figure 3 shows the two-way activity × treatment interactions.

Figures 2 and 3 show some relationships between

Table III. Interference experiments: results of ANOVA for all treatment groups during last two non-experimental observation periods (OP3 and OP5)

Effect	*df*	Sum of squares	*F*	*P*
Observation period	1	1·53	193·5	0·0001
Treatment	3	0·42	17·7	0·0001
Activity	4	24·18	762·7	0·0001
Hour	6	8·91	187·4	0·0001
Observation period × treatment	3	0·47	0·2	0·8990
Observation period × activity	4	1·51	47·5	0·0001
Observation period × hour	6	2·35	49·5	0·0001
Treatment × activity	12	0·39	4·1	0·0001
Treatment × hour	18	0·72	5·0	0·0001
Activity × hour	24	7·29	38·4	0·0001
Observation period × treatment × activity	12	0·35	0·4	0·9736
Observation period × treatment × hour	18	0·19	1·4	0·1353
Observation period × activity × hour	24	2·02	10·6	0·0001
Treatment × activity × hour	72	0·71	1·2	0·0868
Observation period × treatment × activity × hour	72	0·29	0·5	0·9998
Error	3495	27·69		

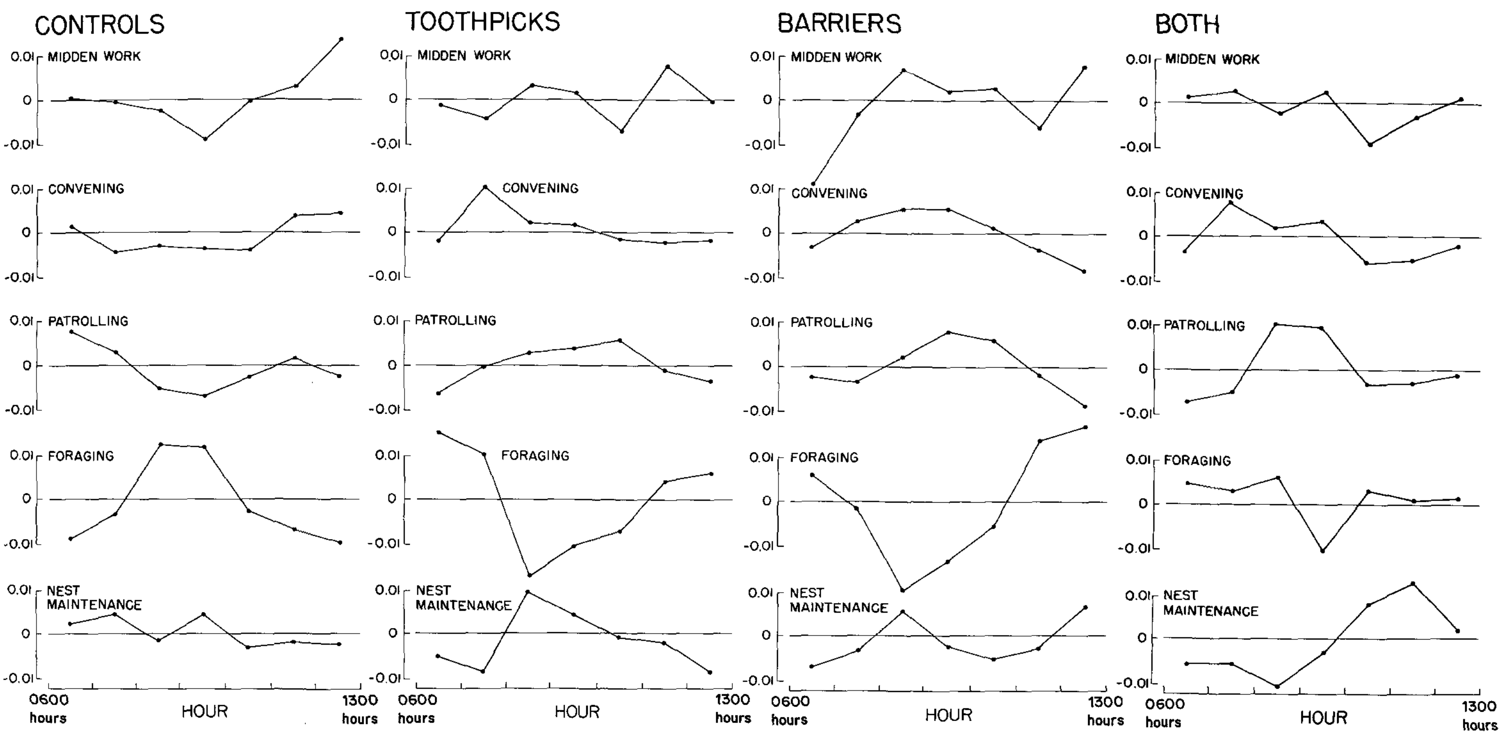

Figure 2. Interference experiments: decompositions of treatment × activity × hour interactions. Each point represents the magnitude of the three-way interaction effect, and thus represents the effect of the treatment on the temporal pattern in that activity.

Table IV. Interference experiments: results of ANOVA for all treatment groups during experimental observation periods (OP2, OP4 and OP6)

Effect	*df*	Sum of squares	*F*	*P*
Observation period	2	4·74	311·2	0·0001
Treatment	3	0·53	23·03	0·0001
Activity	4	43·62	1431·8	0·0001
Hour	6	9·26	202·6	0·0001
Observation period × treatment	6	0·75	16·49	0·0001
Observation period × activity	8	1·98	32·5	0·0001
Observation period × hour	12	1·77	19·3	0·0001
Treatment × activity	12	0·66	7·2	0·0001
Treatment × hour	18	0·66	4·8	0·0001
Activity × hour	24	10·95	59·9	0·0001
Observation period × treatment × activity	24	0·30	1·7	0·0232
Observation period × treatment × hour	36	1·09	3·9	0·0001
Observation period × activity × hour	48	1·63	4·5	0·0001
Treatment × activity × hour	72	1·08	1·97	0·0001
Observation period × treatment × activity × hour	144	0·85	0·77	0·9797
Error	7065	53·8		

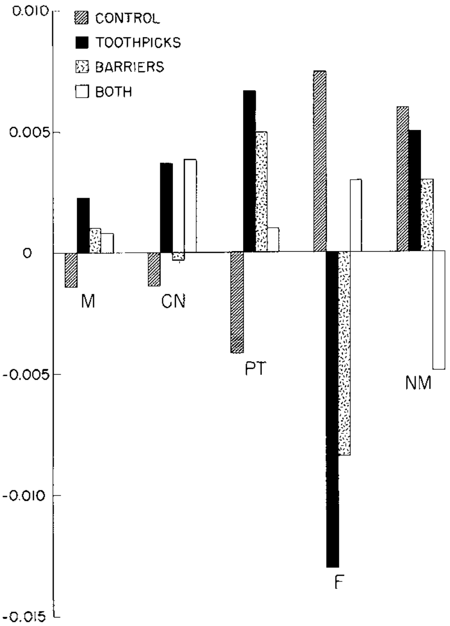

Figure 3. Interference experiments: decompositions of treatment × activity interactions. Each bar represents the magnitude of the two-way interaction effect, and thus represents the effect of the treatment on the mean normalized numbers of ants doing that activity. M = midden work, CN = convening, PT = patrolling, F = foraging, NM = nest maintenance.

treatment and the priorities of various activities. Foraging and nest maintenance seem to be of reciprocal priority. The lines describing the temporal pattern in the effects of the toothpick and barrier treatments on these two activities appear as mirror images of each other (Fig. 2). When colonies respond to either of these treatments with an increase in foraging, there is a decrease in nest maintenance at the same time, and vice versa.

Introducing both toothpicks and barriers did not have an additive effect on nest maintenance and foraging (Figs 2, 3). Furthermore, the effects of the treatment using both were qualitatively different from those of toothpicks or barriers alone (Fig. 2). Introducing toothpicks led to an increase in nest maintenance, as expected, because nest maintenance workers had to move toothpicks and then do ordinary nest maintenance tasks. This treatment also led to an increase in patrolling and convening, and a decrease in foraging (Fig. 3). Barriers, which decreased foraging as expected, caused an increase in nest maintenance, patrolling, and midden work. But the combination of both treatments seemed to force colonies to make a choice, and they chose foraging at the expense of nest maintenance activities. In the ANOVA contrasting each treatment with the controls (Table V), the groups receiving both toothpicks and barriers showed more highly

Table V. Interference experiments: results of a priori ANOVAs comparing controls with each treatment during experimental observation periods (OP2, OP4 and OP6)

		Controls versus toothpicks			Controls versus barriers			Controls versus both		
Effect	*df*	SS*	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Observation period	2	2·50	156·8	0·0001	2·80	167·8	0·0001	2·24	146·7	0·0001
Treatment	1	0·26	33·1	0·0001	0·74	0·9	0·3456	0·37	48·1	0·0001
Activity	4	30·40	960·9	0·0001	30·45	910·4	0·0001	31·52	1033·8	0·0001
Hour	6	6·94	146·0	0·0001	6·47	128·9	0·0001	7·22	157·8	0·0001
Observation period × treatment	2	0·45	28·2	0·0001	0·48	28·7	0·0001	0·09	5·7	0·0034
Observation period × activity	8	1·25	19·8	0·0001	1·09	16·4	0·0001	1·27	20·8	0·0001
Observation period × hour	12	0·66	6·9	0·0001	0·95	9·5	0·0001	0·68	7·4	0·0001
Treatment × activity	4	0·41	12·9	0·0001	0·31	9·3	0·0001	0·13	4·3	0·0018
Treatment × hour	6	0·15	3·2	0·0037	0·39	7·9	0·0001	0·33	7·2	0·0001
Activity × hour	24	7·70	40·7	0·0001	7·90	39·8	0·0001	8·47	47·3	0·0001
Observation period × treatment × activity	8	1·70	2·6	0·0075	0·17	2·6	0·0088	0·05	0·8	0·6314
Observation period × treatment × hour	12	0·37	3·9	0·0001	0·68	6·8	0·0001	0·37	4·0	0·0001
Observation period × activity × hour	48	0·82	2·2	0·0001	1·10	2·7	0·0001	0·86	2·4	0·0001
Treatment × activity × hour	24	0·41	2·2	0·0008	0·57	2·8	0·0001	0·36	1·9	0·0034
Observation period × treatment × activity × hour	48	0·23	0·6	0·9849	0·53	1·3	0·0630	0·25	0·7	0·9495
Error	4775	37·79			39·89			36·43		

* Sum of squares.

significant treatment × activity × hour effects than the controls.

Figure 2 shows a connection between patrolling and foraging. Peaks in the positive deviations for experimental colonies preceded positive deviations in foraging. Increases in foraging as a result of perturbations tended to occur in the latter part of the activity period, as did increased patrolling. There is also a temporal relationship between the deviations in patrolling and midden work in experimental colonies; the peak in the patrolling increase is accompanied or followed by a decrease in midden work.

The effect of increasing the magnitude of the treatment in successive observation periods was confounded with the effect of weather differences and variations of unknown causes in successive observation periods. The significant effects of treatment and treatment × activity × hour in OP3 and OP5, when all colonies were undisturbed (Table III), show that there were still residual effects of treatment during the week-long periods between experiments. Thus it is not possible to tell whether the significant effects involving observation period (Table IV) are a result of climactic or other differences across the observation periods, or increases in the magnitude of perturbations.

REMOVAL EXPERIMENTS

Methods

The study was conducted at the same site, using the same classification of activities (Table I), observation methods, and procedure for normalizing data for colony size, as in the interference experiments described above.

Twelve *P. barbatus* colonies were observed for two 5-day periods, separated by an interval of 4 days, on August 12–16, and August 20–24, 1984. Six of the colonies were left undisturbed as controls. These were the same colonies used as controls in the interference experiments. The other six colonies were divided into three treatment groups of two colonies each. In the first treatment group, 25 nest maintenance workers were removed from each colony; in the second, 25 foragers were removed; in the third, 25 of each were removed. Two such series of removals were made, one on the third day of each 5-day period, 9 days apart. In each of the two series of removals, colonies were observed for 2 days before removal and on the 2 days following. Each of these four 2-day periods is an observation period. Because of a decrease in colony activity, only 12 (instead of 25) nest maintenance workers were removed in one of the colonies in the first treatment group, in the second removal.

Twenty-five foragers represent 43% of the mean maximum number of foragers observed in undisturbed colonies within 1·3 m of the nest entrance, and this number is estimated to be less than 20% of the total number of foragers outside the nest. Twenty-five nest maintenance workers represent 62% of the mean maximum for nest maintenance work, and since all nest maintenance work is done within the area observed, this can be considered to be 62% of the work force devoted to nest maintenance outside the nest. Nest maintenance workers were removed with an aspirator when returning to the nest, after they had come out of it bearing sand, and had put it down. Foragers were removed while proceeding directly along a trunk trail either to or from the nest.

Each of the 12 colonies were observed once each hour during the morning activity period, from 0600 to 1300 hours. Observations made on the days when removals were done were not used in the analysis, because aspirating ants disrupted the colony's behaviour. A total of 460 observations were used in the analysis.

The data for undisturbed and experimental colonies were first analysed separately. In the undisturbed colonies, a three-way full factorial ANOVA (SAS 1982) was done with activity, hour and observation period as main effects. A priori comparisons were made between the observation periods before and after the days that ants were removed from experimental colonies.

The behaviour of each colony before and after each removal was compared by subtracting the numbers for each activity and hour as follows: day 4 − day 1, day 5 − day 2 (day 3 was the day of removals). Thus the behaviour of colonies before removals was used as a control and compared with their behaviour after removals. The differences were normalized and transformed as described above, and used in a four-way, full factorial ANOVA with treatment, removal number (first or second), activity and hour as main effects (BMDP 1981, P4V).

The data for undisturbed and experimental colonies were compared using differences before and after removals, derived for undisturbed col-

Table VI. Removals: mean differences in each activity after removal

	Midden work	Convening	Patrolling	Foraging	Nest maintenance
Undisturbed colonies	−0·0075	−0·0010	−0·0151	−0·0185	−0·0155
Nest maintenance workers removed	−0·0153	−0·0066	−0·0173	−0·0015	−0·0248
Foragers removed	−0·0181	−0·0008	−0·0259	−0·0043	−0·0249
Both removed	−0·0193	−0·0001	−0·0154	−0·0183	−0·0502
Mean for all three removal treatments	−0·0176	−0·0024	−0·0195	−0·0080	−0·0333

onies as described above for the experimental ones. These data were used in a three-way, full-factorial ANOVA (SAS 1982) with treatment, activity and hour as main effects. A priori contrasts were made, comparing each of the experimental treatments with the undisturbed treatment.

Results

In response to all three removal treatments, the numbers engaged in all activities decreased (Table VI). Thus the removal of workers in one activity affected the numbers doing other activities. These decreases are apparent in undisturbed colonies as well, due to seasonal or environmental factors, but are clearly larger in experimental colonies. There were various significant interactions in the ANOVA using differences after removals in experimental colonies (Table VII). This shows that removals had a significant effect; the differences are not statistically equivalent to zero.

The effect of removals was subject to daily activity rhythms. Figures 4 and 5 show the activity rhythms of undisturbed and experimental colonies, before and after removals. The activity period was shifted towards later in the day in the course of the experiment (Fig. 4). Removals intensified this shift, especially in nest maintenance and patrolling (Fig. 5). Figure 6 shows the temporal pattern in the differences in the numbers of ants in each activity, in the experimental colonies. There was a significant activity × hour interaction in the differences in the numbers of ants in each activity after removals (Table VII). All activities decreased early

Table VII. Removals: results of ANOVA for differences (after removals) in experimental colonies

Effect	*df*	Sum of squares	*F*	*P*
Removal number	1	0·05	1·4	0·2344
Treatment	2	0·11	1·5	0·2228
Activity	4	0·81	5·4	0·0003
Hour	6	2·31	10·3	0·0001
Removal number × treatment	2	0·10	1·3	0·2621
Removal number × activity	4	0·16	1·05	0·3821
Removal number × hour	6	1·02	4·5	0·0002
Treatment × activity	8	0·34	1·1	0·3374
Treatment × hour	12	0·37	0·8	0·6196
Activity × hour	24	1·54	1·7	0·0187
Removal number × treatment × activity	8	0·11	0·4	0·9395
Removal number × treatment × hour	12	0·36	0·8	0·6363
Removal number × activity × hour	24	1·17	1·3	0·1547
Treatment × activity × hour	48	0·78	0·4	0·9997
Removal number × treatment × activity × hour	48	0·89	0·5	0·9984
Error	610	22·83		

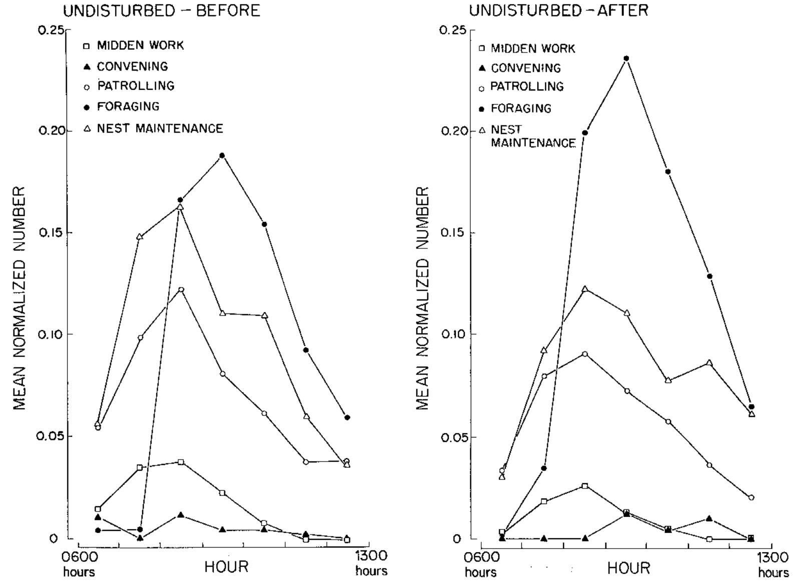

Figure 4. Removals: activity rhythms of undisturbed colonies before and after removals. Each point represents the mean normalized numbers of ants in a particular activity and hour before removals (OP1 and OP3) or after removals (OP2 and OP4).

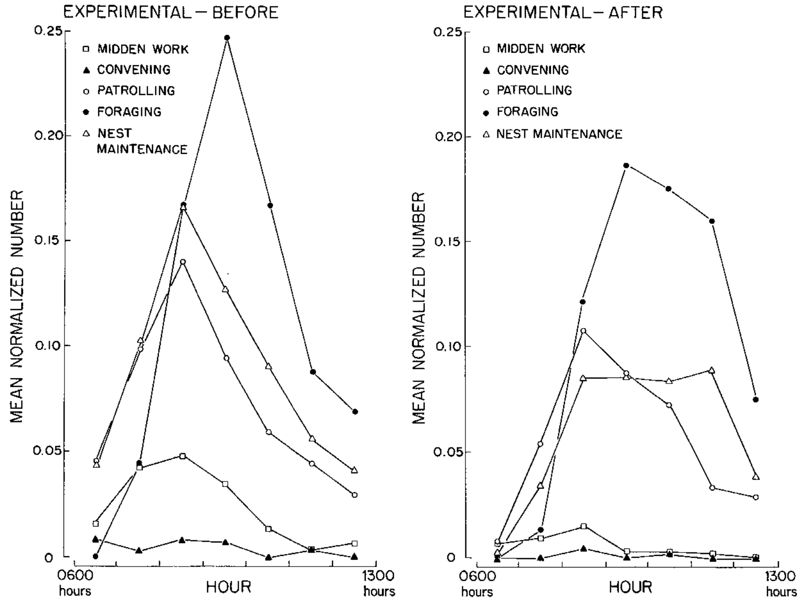

Figure 5. Removals: activity rhythms of experimental colonies before and after removals. Each point represents the mean normalized numbers of ants in a particular activity and hour before removals (OP1 and OP3) (left graph) or (right graph), after removals (OP2 and OP4). Data are averaged over all three experimental treatments.

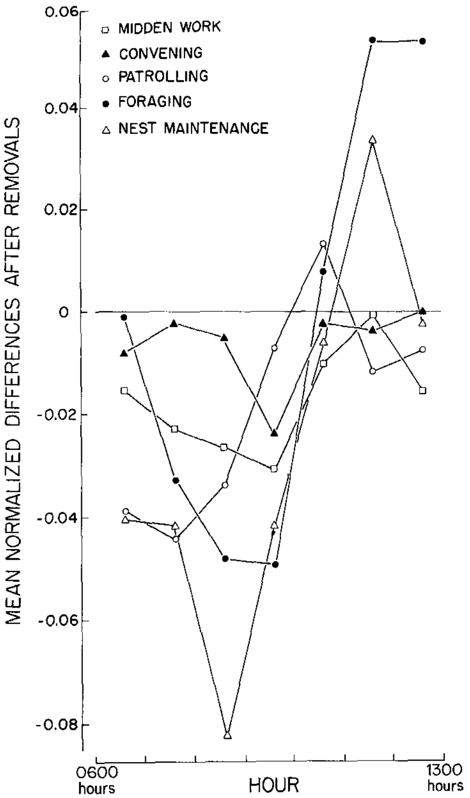

Figure 6. Removals: differences after removals in experimental colonies. Each point represents the mean difference in normalized numbers of ants in a particular activity and hour, after removals. Shown are the means of differences in both the first removal (OP2 − OP1) and second removal (OP4 − OP3). Data are averaged over all three experimental treatments.

in the day, then increased later on. Thus the effects of removals depends on both activity and time of day.

Removals had different effects on each activity (significant activity effect, Table VII). Figure 7 shows the effect of removals on each treament group. Removals had the smallest effect on the numbers convening, which were small to begin with. The largest differences were in the numbers doing nest maintenance.

Although the treatment × activity interaction was not significant (Table VII), there are still some interesting trends in the data which reflect the relative priorities of nest maintenance and foraging. In all treatments, foraging decreased much less (mean difference = −0·0080) than nest maintenance (−0·0333). Figure 7 reveals another relationship between these two activities. Removing both nest maintenance workers and foragers caused a larger decrease in the proportions of ants doing each of these activities than removing only nest maintenance workers or foragers.

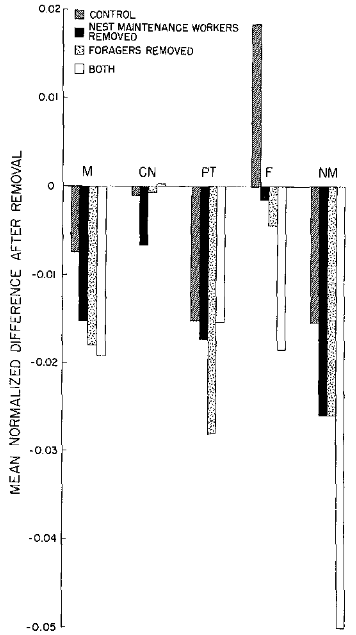

Figure 7. Removals: differences in activity means after removals. The figure shows the data presented in Table VI. Each bar represents the mean difference after removals in one activity, and in one treatment group.

Figure 8 shows the differences displayed in Table VI and Fig. 7, with the mean effect or difference for undisturbed colonies subtracted out. For example, the decrease in foraging shown in Fig. 8 has the overall increase in foraging observed in undisturbed colonies subtracted out. The figure shows that nest maintenance decreased more when both maintenance workers and foragers were removed, relative to the removal of each group separately, than foraging.

Colonies responded similarly to the removal of nest maintenance workers and foragers, or both (no significant effects involving treatment, Table VII). Removing the second groups of workers caused behavioural differences similar to those caused by removing the first group of 25 (no significant effect of removal number, Table VII). That is, the effect of removals was not cumulative over the 9 days that elapsed between removals.

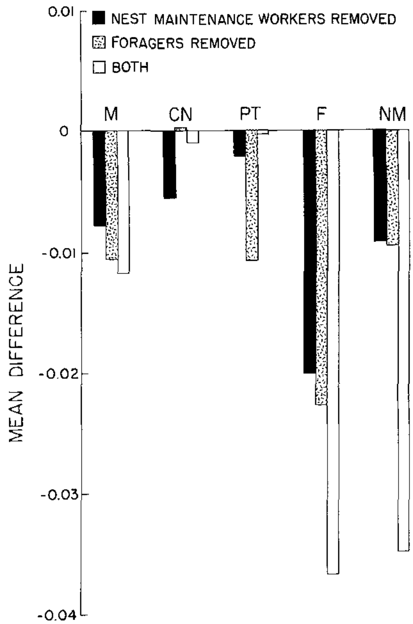

Figure 8. Removals: corrected differences in activity means after removals. The same mean differences are shown as in Fig. 7, except that the mean difference for each activity in undisturbed colonies is subtracted from the difference for that activity, in each experimental group.

The behaviour of the undisturbed colonies varied across observation periods, leading to significant main and interaction effects (Table VIII). The a priori comparisons show that the behaviour of these colonies in the days before the first removal were significantly different from their behaviour afterwards; this was not the case for the second removal.

The results of the comparison between experimental and undisturbed colonies are shown in Table IX. The significant treatment effect when the undisturbed treatment is included (Table IX), in conjunction with the absence of a significant treatment effect across the three experimental treatments alone (Table VII), means that experimental and undisturbed colonies differed significantly in response to removals. The a priori tests show that the behavioural effects in all three treatments, presumably due to removals, were significantly different from the changes in behaviour seen in undisturbed colonies, presumably due to climactic factors.

DISCUSSION

Clearly, changes in the behaviour of one worker group led to changed patterns in the behaviour of other worker groups. This means that in investigating other aspects of ant biology, such as division of labour or foraging ecology, particular activities cannot be understood in isolation from each other. Perturbations caused changes in the temporal patterns of various activities. In future experiments examining the consequences of perturbing some activity or removing certain workers, it would be

Table VIII. Removals: results of ANOVA for undisturbed colonies

Effect	*df*	Sum of squares	*F*	*P*
Activity	4	19·0	375·2	0·0001
Hour	6	5·14	67·6	0·0001
Observation period	3	3·76	96·0	0·0001
Activity × hour	24	5·54	18·2	0·0001
Activity × observation period	12	1·40	9·2	0·0001
Hour × observation period	1	0·65	2·8	0·0001
Activity × hour × observation period	72	1·20	1·3	0·0415*
First removal	1	0·10	8·0	0·0047
Second removal	1	0·03	2·7	0·1000
Error	1540	19·54		

* The activity × hour × observation period interaction should not be considered significant in undisturbed colonies. Some activity × hour cells had a variance of 0 because no ants ever did that activity in that hour. The resulting heterogeneity of variance requires a conservative interpretation of the results.

Table IX. Removals: results of ANOVA for differences (after removals) in experimental and undisturbed colonies

Effect	*df*	Sum of squares	*F*	*P*
Activity	4	0·81	7·1	0·0001
Hour	6	1·98	11·5	0·0001
Treatment	3	1·25	14·4	0·0001
Activity × hour	24	1·21	1·8	0·0132
Activity × treatment	12	0·64	1·9	0·0365
Hour × treatment	18	1·09	2·1	0·0045
Activity × hour × treatment	72	1·61	0·8	0·9164
Error				
A priori comparisons				
Undisturbed versus nest maintenance workers removed	1	0·34	11·9	0·0006
Undisturbed versus foragers removed	1	0·49	17·3	0·0001
Undisturbed versus both removed	1	0·92	31·9	0·0001
Error	1515	43·59		

useful to consider not only the effect on the number of workers engaged in other activities, but also the effect upon the temporal patterns of these activities. This is a general methodological point, based on the finding that various activities are interrelated. The results on particular relationships among activities reveal some interesting aspects of the social organization of *P. barbatus* colonies.

The results imply a reciprocal relationship between nest maintenance and foraging. In the interference experiments, an increase in one is accompanied by a decrease in the other. When both activities are interfered with, the colony chooses foraging instead of nest maintenance. When workers are removed, two results suggest that foraging is given higher priority than nest maintenance in the recruitment of new ants. First, foraging decreased less in response to removals than did nest maintenance or other activities except convening (Table VI). Second, the decrease in nest maintenance when both types of workers were removed was larger, relative to the decrease in nest maintenance when each type was removed, than the analogous decrease in foraging (Fig. 8). In other words, foraging decreased less than nest maintenance when workers in both groups were removed.

The mechanisms underlying the relationship between foraging and nest maintenance are not known. Rapid recruitment to make up for colony losses seems to be the rule for several ant genera (Wilson 1983, 1984). Where do the ants recruited to a new task come from? Wilson (1983) reported that the workers of *Atta cephalotes* recruited replacements for removed foragers from a group of workers that accompanied foragers on their excursions and waited nearby, but did not ordinarily forage themselves. Work on other *Pogonomyrmex* species suggest that in this genus, however, reserve workers usually remain inside the nest (MacKay 1981; Porter & Jorgensen 1981). In other harvester ant species, experiments with marked individuals show that nest maintenance and foraging are done by different ants (Porter & Jorgensen 1981; Gordon 1984c). In the present work, though further experiments with marked individuals are needed to confirm this, the results of the removal experiments (Fig. 7) suggest that when large numbers of workers are newly recruited into either of these groups, they are recruited from a common pool of possible foragers or nest maintenance workers.

Figure 7 indicates that the pool of reserve workers is not divided into two separate classes of potential nest maintenance workers and foragers. If the pool were so divided, the removal of nest maintenance workers should have had the same effect whether or not foragers were removed as well. Similarly, the removal of foragers should not be affected by the simultaneous removal of nest maintenance workers. The result that, in both cases, removing both types of workers has a stronger effect (causes numbers doing both the tasks to decrease more) than when only one type was removed, suggests that new ants are recruited into both tasks from a common pool. If new workers were needed to do both tasks, it appears that fewer workers were available than if only one type was needed.

However, the numbers of reserve workers inside the nest were probably large relative to the fluctuations in numbers seen in this study (MacKay 1981). Thus, the reciprocal relationship between nest maintenance workers and foragers should not be considered a simple consequence of a constraint on the number of available individuals. Experiments with marked individuals are needed to clarify the mechanisms underlying the relation between nest maintenance and foraging. At the colony level it seems that some perturbations elicit either predominantly foraging or predominantly nest maintenance responses.

Although the perturbations caused widespread changes in activity rhythms, certain aspects of the latter were preserved. For example, in the interference experiments, patrolling increased in response to all of the treatments (Fig. 3). The timing of this increase (Fig. 2) is related to the temporal pattern in foraging. In undisturbed colonies, the peak in patrolling precedes the peak in foraging, and it is during the peak in patrolling that most workers are recruited to new food sources (Gordon 1983b). Foragers already travelling to a common foraging site will not digress when a new food source is presented later in the day, after patrolling activity has subsided. In the interference experiments, the increase in patrolling caused by perturbations preceded the increase in foraging. Similarly, after removals, the peak in patrolling still preceded the peak in foraging (Fig. 5). Thus the temporal relationship between patrolling and foraging was preserved, suggesting that the use of patrollers to advise the foragers of new food sources is an important element of colony organization.

Removing nest maintenance workers caused a decrease in the numbers of ants foraging and patrolling. There is evidence that patrolling and nest maintenance are done by different ants in other *Pogonomyrmex* species (Porter & Jorgensen 1981; Gordon 1984c). There is no indication that new patrollers come from the same reserve group as nest maintenance workers and foragers. The interference experiments suggest a relationship between increased foraging and increased patrolling. The removal experiments indicate the converse, that decreased foraging leads to decreased patrolling.

Previous research suggests that midden work and patrolling are done by the same ants (Gordon 1984c). In all treatment groups in the interference experiments, midden work decreased as or after patrolling increased (Fig. 2), indicating that midden work is of lower priority than patrolling. Midden work decreased as a consequence of removals. This may be linked to decreased foraging, since a smaller flow of seeds into the colony means that midden workers have smaller amounts of husks to take care of.

The decrease in activity following removals is consistent with previous results of predation experiments in other *Pogonomyrmex* species. Removing small numbers of ants generally causes decreased activity as observed here (Gentry 1974), while removing larger numbers causes ants to stop coming out altogether (MacKay 1982; Munger 1984). Removing larger numbers of ants would probably have caused a cessation of *P. barbatus* activity as well.

This work raises many further questions concerning the mechanisms at the individual level which will explain the behaviour observed here. For example, do individuals switch tasks in the face of perturbations, as they do in some other ant species (Meudec & Lenoir 1982; Wilson 1984)? How do individuals communicate that more or fewer workers are needed? Do increased numbers of patrollers stimulate more foragers, or do the conditions inside the nest preceding increased foraging stimulate more patrollers? Experiments with marked individuals are needed to explore these questions.

At the colony level, this study only begins to elucidate the dynamics of the organization of harvester ant society. One crucial question left unresolved concerns the duration of response to perturbations. In the interference experiments, colonies left undisturbed for a week still showed altered daily rounds (Table III). On the other hand, the absence of cumulative effects in the removal experiments indicates that 9 days is enough for a colony to respond to the loss of a significant part of the outside work force in each group. When the recovery time of a colony is known, it will be possible to test the effects of perturbations of increasing magnitude.

Interfering with other colony activities would reveal more about the relative priorities of each activity. Considerable research has been done on the foraging ecology of harvester ants, especially on interference competition for food (e.g. Davidson 1977, 1980; DeVita 1979). The present study sheds some light on the relative priority of foraging and other activities in *P. barbatus*. When such priorities are understood for other species, it may be possible to test predictions about the behavioural interactions caused by competition for food. That is, we may be able to ask in detail, how does the foraging behaviour of one species affect the daily rounds, including foraging behaviour, of neighbouring species? More generally, we know that biotic events, such as variations in food supply, predation or destruction of the nest by other animals, affect the distribution and abundance of ant colonies (Holldobler 1976; Whitford et al. 1976; MacKay 1982). But to predict ecological effects, it would be useful first to know the dynamics relating environmental events and colony behaviour.

APPENDIX

In a three-way ANOVA, the mean for the cell AHT_{ijk} is

$$AHT_{ijk} + m + a_i + t_j + h_k + at_{ij} + ah_{ik} + th_{jk} + aht_{ijk}$$

where m is the overall mean, a_i is the effect of the ith activity, t_j is the effect of the jth treatment, and h_k is the effect of the kth hour. A_i is the weighted mean for the ith activity, and also for T_j and H_k. AT_{ij} is the weighted mean of the interaction between the ith activity and the jth treatment, and so on for the other two-way interaction means.

The magnitudes of the interaction effects (Figs 2, 3) were calculated as follows, using the procedure of Brooks (1985). Capital letters represent observed means, and small letters represent effects. A, H, and T denote activity, hour and treatment, respectively.

(1) Overall mean: m = mean of all values.

(2) Main effects.

$$\begin{aligned} a_i &= A_i - m \\ t_j &= T_j - m \\ h_k &= H_k - m \end{aligned}$$

(3) Two-way interactions.

$$\begin{aligned} at_{ij} &= AT_{ij} - a_i - t_j - m \\ ah_{ik} &= AH_{ik} - a_i - h_k - m \\ th_{jk} &= TH_{jk} - t_j - h_k - m \end{aligned}$$

(4) Three-way interaction.

$$aht_{ijk} = AHT_{ijk} - at_{ij} - ah_{ik} - th_{jk} - a_i - h_k - t_j - m$$

ACKNOWLEDGMENTS

I am very grateful to L. D. Brooks for designing the statistical analysis, guiding me through it, and inventing a graphical representation of the results. I thank N. Forsthoefl for help with the field work; R. Levins, E. O. Wilson, and D. S. Burdick for valuable discussions; and L. Roseman for his patience and help with the computer graphics, which were supported by P. J. Huber's 'Interactive graphical analysis of high-dimensional data' project. Data analysis was made possible by a rescue from the staff at Harvard Office of Information Technology, especially B. Weber. J. R. Gregg, J. Herbers and B. Waldman provided very useful criticisms of the manuscript. R. C. Lewontin made generous contributions, both intellectual and practical, to all stages of the project, which improved it greatly. The project was supported by a Junior Fellowship from the Harvard Society of Fellows and a research grant from the American Philosophical Society.

REFERENCES

Brooks, C. D. 1985. The organization of genetic recombination in *Drosophila melanogaster*. Ph. D. thesis, Harvard University.

Davidson, D. W. 1977. Foraging ecology and community organization in desert seed-eating ants. *Ecology*, **58,** 725–737.

Davidson, D. W. 1980. Some consequences of diffuse competition in a desert ant community. *Am. Nat.*, **116,** 92–105.

DeVita, J. 1979. Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Majave desert. *Ecology*, **60,** 729–734.

Dixon, W. (Ed.) 1981. *BMDP Statistical Software.* Berkeley: University of California Press.

Gentry, J. B. 1974. Response to predation by colonies of the harvester ant, *Pogonomyrmex badius*. *Ecology*, **55,** 1328–1338.

Gordon, D. M. 1983a. Daily activity rhythms in social activities of the harvester ant, *Pogonomyrmex badius*. *Psyche*, **90,** 413–423.

Gordon, D. M. 1983b. The relation of recruitment rate to activity rhythms in the harvester ant, *Pogonomyrmex barbatus*. *J. Kans. Entomol. Soc.*, **56,** 277–285.

Gordon, D. M. 1983c. Dependence of necrophoric response to oleic acid on social context in the ant, *Pogonomyrmex badius*. *J. Chem. Ecol.*, **9,** 105–111.

Gordon, D. M. 1984a. Species-specific patterns in the social activities of harvester ant colonies. *Insectes soc.*, **31,** 74–86.

Gordon, D. M. 1984b. Harvester ant middens: refuse or boundary? *Ecol. Entomol.*, **9,** 403–412.

Gordon, D. M. 1984c. The persistence of role in exterior workers of the harvester ant, *Pogonomyrmex badius*. *Psyche*, **91,** 251–266.

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

MacKay, W. P. 1981. A comparison of the nest phenologies of three species of harvester ants (Hymenoptera: Formicidae). *Psyche*, **88,** 25–74.

Mackay, W. P. 1982. The effect of predation of western widow spiders (Araneae: Theridiidae) on harvester ants (Hymenoptera: Formicidae). *Oecologia*, **53,** 406–411.

Meudec, M. & Lenoir, A. 1982. Social responses to variation in food supply and nest suitability in ants (*Tapinoma erraticum*). *Anim. Behav.*, **30,** 284–292.

Munger, J. C. 1984. Long-term yield from harvester ant colonies: implications for horned lizard foraging. *Ecology*, **65,** 1077–1086.

Porter, S. D. & Jorgensen, C. D. 1981. Foragers of the harvester ant, *Pogonomyrmex owheei*: a disposable caste? *Behav. Ecol. Sociobiol.*, **9,** 247–256.

Whitford, W. & Ettershank, G. 1975. Factors affecting foraging activity in Chihuahuan desert harvester ants. *Env. Entomol.*, **4,** 689–696.

Whitford, W. G., Johnson, P. & Ramirez, J. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Insectes soc.*, **23,** 117–132.

Wilson, E. O. 1983. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). III. Ergonomic resiliency in foraging by *A. cephalotes*. *Behav. Ecol. Sociobiol.*, **14,** 47–54.

Wilson, E. O. 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, **16,** 89–98.

(Received 27 July 1985; revised 4 October 1985; MS. number: A4524)