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Dynamics of task switching in harvester ants

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Abstract. Harvester ants, *Pogonomyrmex barbatus*, were marked when engaged in one of four activities outside the nest: foraging, patrolling, nest maintenance and upkeep of the colony refuse pile. In undisturbed older colonies, each activity was done by a distinct group of workers. In undisturbed younger colonies, nest maintenance workers were likely to forage. Further experiments examined the conditions under which workers of each task group engaged in other activities. Marked workers were observed in the course of perturbations that increased the numbers engaged in one activity. In response to perturbations, most workers would switch tasks to forage, and nest maintenance workers were likely to switch to other tasks. Previous work showed that changes in the numbers of ants engaged in one activity alter the numbers engaged in other activities. The experiments with marked individuals described here show that task switching among exterior workers does not account for the observed responses to perturbations. This means that within a time scale of several hours, one worker group receives information about events affecting other worker groups.

In social insect colonies, workers tend to specialize in particular tasks. In some polymorphic ant species, workers of a certain size do fixed tasks throughout their adult lives (e.g. Wilson 1980). Most ant genera are monomorphic, and in many monomorphic species, a worker's task changes (over weeks or months) as she gets older. Specialized groups of workers, classified by size or age, are known as 'behavioural subcastes'. Current theory on the evolution of social insects (e.g. Wilson 1968, 1985) views colonies as divided into groups of workers of fixed task. The theory assumes that a colony's behaviour is determined by two characteristics of each behavioural subcaste: how many workers it contains, and how efficient its workers are at doing their task. This assumption provides the link between ecological and evolutionary arguments. For example, when ecological conditions make increased foraging adaptive, colonies should evolve larger, more effective foraging castes (Oster & Wilson 1978).

However, recent studies show that caste distributions do not fully predict colony behaviour. A colony's response to ecological conditions seems also to depend on dynamics at two, interrelated levels. First, at the individual level, there are the dynamics that determine changes in the task of each individual. In both polymorphic and monomorphic species, individuals change tasks in response to either short-term emergencies (Meudec & Lenoir 1982) or longer-term changes in the numbers available of each worker type (Wilson 1984). Second, at the colony level, there are the dynamics of colony effort, which determine changes in the distribution of workers into various tasks. In honey bees, *Apis mellifera*, for example, the numbers of workers allocated to foraging vary as colony requirements change (e.g. Winston & Punnett 1982; Kolmes 1985; Seeley 1986). Thus the amount of foraging a honey bee colony does is not a simple function of the numbers present in a foraging caste. Here I investigate task switching in harvester ants, *Pogonomyrmex barbatus*, and its relevance to colony-level changes in the numbers of workers allocated to different tasks.

Harvester ant colonies engage in various tasks outside the nest. These include foraging, travelling along cleared trails to collect seeds and insect parts; patrolling the nest mound and trails; nest maintenance, both clearing sand out of the nest and clearing the mound and trails of vegetation; and midden work, the sorting and upkeep of the colony refuse pile, or midden. These activities are done each day in a characteristic temporal sequence while the colony is active outside the nest (Gordon 1984a). In the summer, *P. barbatus* colonies are active outside the nest from sunrise until about noon, when high temperatures force them back

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into the nest. Though mature colonies can contain up to 10 000 workers (MacKay 1981), exterior workers can be considered to be a discrete subset of the colony. They rarely mix with the interior workers (Gentry 1974; Porter & Jorgensen 1981; MacKay 1983) who remain in the lower levels of the nest, engaged in brood care, food storage and the upkeep of the nest structure.

In the present study, I first examined whether exterior workers in undisturbed field colonies of *P. barbatus* specialize in particular tasks. Next I examined whether environmental change leads to task switching. Perturbation experiments with this species have shown that events that directly affect only workers engaged in one task cause changes in the intensity and temporal patterns of other tasks (Gordon 1986, 1987). The mechanism of colony response to perturbation is not understood, but may be mediated by task switching. For example, perturbations causing an increase in numbers of workers doing nest maintenance also cause a decrease in numbers foraging. This could happen because foragers switch to nest maintenance.

Only about 25% of a harvester ant colony works outside the nest (MacKay 1983), but occasionally unusually large numbers of workers will emerge to perform some task. Many ant species, including others in the genus *Pogonomyrmex*, maintain a group of reserve workers inside the nest (reviewed in Porter & Jorgensen 1981), and it seems likely that this is true in *P. barbatus* as well. The results described above, significantly increased numbers doing nest maintenance, could be caused by the recruitment of previously inactive workers from inside the nest. This raises the question whether the extra workers that emerge in response to perturbations are themselves committed to particular tasks. A third set of experiments addressed this question.

Previous experiments showed that interactions between worker groups in response to perturbations change as a colony gets older (Gordon 1987). For example, compared with younger colonies (1–2 years old), older ones (at least 5 years old) showed a more consistent response to successive trials of a given perturbation. Here I compared the ways that workers change task in younger and older colonies.

METHODS

The study was conducted at the same site used for previous work (Gordon 1986, 1987) near Portal, Arizona, in June–August 1986 and June–August 1987. Ants were marked with Pactra hot fuel-proof model airplane paint. In 1986, ants were taken into the laboratory, marked, kept overnight, and returned the next day. In 1987, ants were marked in the field and returned to the colony within 2 h. A few marked ants were kept for a week in the laboratory, and neither these ants nor any ants observed in the field ever seemed to be affected by the paint after it had dried.

Foragers were collected when they were returning to the nest, on a foraging trail, carrying a seed or other food item; nest maintenance workers were collected after they had come out of the nest entrance, carrying a bit of sand, and had put the sand down on the nest mound; patrollers were collected after they had walked around on the nest mound in a characteristic zig-zag trajectory, often with the abdomen tucked beneath the thorax, and had made antennal contact with at least two other ants; midden workers were collected after picking up an item from the refuse pile, or midden, and had put it down somewhere on the midden. (Activities of exterior workers are described in detail in Gordon 1986.) Each activity was assigned a unique colour of paint and ants were marked according to the activity they were engaged in when collected. Collecting and marking sufficient numbers of workers took 3–4 days per colony in 1986, and 1–2 days in 1987. All observations were made the day after marking was finished. An observation of a given colony consisted of recording, for each activity, the numbers of marked and unmarked ants engaged in it. Observations of each colony were made at intervals of 8–10 min throughout the morning activity period, a total of 30–40 observations per colony per day. Most trips outside the nest, except by foragers, last less than 2 min and 10 min is a sufficiently long interval for an ant engaged in one task to begin doing another.

Table I shows the number of colonies, and which ants were marked, in each experiment. In all experiments, the same number of ants were marked in each activity for which marking was done. Thus, differences in numbers of ants marked in one task, and later observed in other tasks, could not arise simply from differences in the numbers marked. Fewer workers engage in midden work than in the other activities (Gordon 1984a), and many younger colonies do not have a midden at all. If it was not possible to mark as many midden workers as the number marked in other activities, midden workers

Table I. List of experiments

Treatment	Year	Colony age	Number of colonies	Numbers of ants marked per colony						
				M	PT	F	NM	EPT	EF	ENM
Undisturbed	1986 and 1987	O	7	50	50	50	50			
Undisturbed	1986	Y	6		50	50	50			
Perturbations										
F increased	1987	O	5	50	50	50	50			
NM increased	1986	O	3	50	50	50	50			
NM increased	1986	Y	5		50	50	50			
PT increased	1987	O	4	50	50	50	50			
Extras										
(extras marked/experimentally increased)										
F/PT	1987	O	2			100			100	
F/NM	1987	O	3			100			100	
NM/F	1987	O	4				50			50
NM/PT	1987	O	2				50			50
PT/NM	1987	O	3		50			50		
PT/F	1987	O	3		50			50		

O: older colonies; Y: younger colonies; M: midden work; PT: patrolling; F: foraging; NM: nest maintenance; EPT: extra patrollers; EF: extra foragers; ENM: extra nest maintenance workers. See text for further explanation.

were not marked. Midden workers were never marked in younger colonies. Colony age was estimated using maps and records from previous years, and measurements of nest size (estimation methods described in Gordon 1986). A total of about 7500 ants from 44 colonies was marked.

One of the results, described below, shows that the sample sizes used here are sufficient. In undisturbed colonies, ants marked from one activity are not later distributed randomly in other activities. Thus a sample of ants collected when engaged in one activity can be considered as a sample of a sub-group devoted to that task. The sample sizes (50 ants per activity for most experiments, 100 for foragers in experiments with marked extras) appear to be fairly large relative to the numbers of ants available from one day to the next for each exterior task. It is rare to see more than 50 midden workers, patrollers or nest maintenance workers at a time. In many colonies, after 50 workers from each of the latter three tasks were marked, often more than half of the ants observed in each of these activities were marked ants. This suggests that for these three activities, 50 marked ants constituted a substantial proportion of the unknown total number of ants available from one day to the next to do each of these tasks. Larger numbers of foragers (100, Table I) were marked in some experiments because larger numbers of foragers (up to about 800 in large colonies at the peak of a very active day) are seen outside the nest.

Because the marking technique did not distinguish between individuals, it was not possible to assess variation among individuals in activity level. However, sufficiently large numbers were observed simultaneously outside the nest to rule out the possibility that tasks were done by only a few marked individuals. In younger colonies, more than 15 marked ants per activity were often observed simultaneously; in undisturbed colonies, 5–10 per activity; and in perturbations that intensified patrolling or foraging, often 15–20 per activity.

The experiments were as follows.

(1) Undisturbed colonies. These were used to determine whether ants in undisturbed colonies continue to do the task they were engaged in when marked.

(2) Perturbation experiments were performed to determine whether perturbations result in task switching. The following perturbations were carried out in colonies with marked workers.

(a) Increased intensity of foraging. Foraging was intensified by placing small piles (about 2 tablespoons) of mixed seeds outside the nest mound, away from the foraging trails. Since recruitment to new food sources is done by patrollers, before foragers are active on the trails (Gordon 1983), seeds were placed in front of scouting patrollers early in the morning. Active recruitment took place and large numbers of ants participated in trails to the seed sources. Seeds were replenished until 0830 hours.

(b) Increased intensity of nest maintenance. Nest maintenance was intensified as in Gordon (1986, 1987) by placing toothpicks (250 for older colonies, 150 for younger ones) near the nest entrance, at the beginning of nest maintenance activity early in the morning. This causes a significant increase in numbers engaged in nest maintenance, relative to numbers in undisturbed colonies (Gordon 1986, 1987). Toothpicks were moved by the ants to the edge of the nest mound within about an hour, and then ignored.

(c) Increased intensity of patrolling. Patrolling was intensified as in Gordon (1987): 10 workers of the sympatric harvester ant *Novomessor cockerelli*, which interacts agonistically with *P. barbatus* (Gordon 1988), were placed on the nest mound when patrollers were beginning to emerge. In addition, two small cardboard cylinders, anchored by a wire stake, were placed near the nest entrance. Both of these perturbations cause increased numbers patrolling relative to those in undisturbed colonies; patrollers chase the *N. cockerelli* away and attempt, unsuccessfully, to remove the cylinder.

The perturbations conducted here are of the same magnitude as naturally occurring events in a colony's environment: rain and wind wash debris onto nest mounds and foraging trails; ants of other species go onto *P. barbatus nests*; and climatic changes cause fluctuations in seed availability.

(3) Task switching by newly recruited extra workers. The preceding two sets of experiments showed that in undisturbed colonies, workers rarely switch tasks, but in response to perturbations some classes of workers often do. Previous experiments showed that perturbations significantly increase the numbers engaged in certain tasks (Gordon 1986, 1987). I refer to the workers that make up the difference between the numbers seen in undisturbed and perturbed colonies as 'extra' workers. I refer to workers active in undisturbed colonies as 'regular' workers. There are two possible sources for extra workers. First, they could be workers previously active outside the nest doing other tasks that have switched tasks in response to perturbations. Second, they could previously have been inactive inside the nest. If the latter, they could come from a common pool of reserve workers or from distinct groups of inactive reserves, each group committed to a particular task. It was not possible to determine the sources of extra workers, though the results, described below, suggest a hypothesis. Instead, I examined whether an ant that joins the extra workers recruited to a task remains committed to that task.

Experiments were conducted to determine how ants recruited when one task is experimentally intensified later respond to a perturbation of another task. Each experiment took 3 days; observations were made on the last day. On day 1, ants engaged in activity A were marked. Sample sizes were the same as those that appeared to include most active midden workers, patrollers and nest maintenance workers in undisturbed colonies, and the numbers of marked regular foragers were doubled (Table I). On day 2, a perturbation was done that is known to increase the numbers engaged in activity A, in order to elicit the emergence of extra workers. Perturbations were the ones described above. In the course of the perturbation on day 2, ants not marked on day 1, and engaged in activity A, were marked with a second colour. This second group, marked on day 2, is defined as the 'extra' group. On day 3, another, different perturbation was done, known to increase significantly the numbers of ants engaged in another activity, activity B. Colonies were observed on day 3 to see whether the marked extras of activity A would respond to the experimentally induced increase in activity B, by doing activity B. The experiments tested whether marked extras of each of three activities, foraging, patrolling and nest maintenance, would switch to either of the remaining two activities. These six experiments are listed in Table I.

RESULTS

Figures 1–3 show the results for all experiments. For each colony, day and activity I calculated the proportion of marked ants observed to be engaged in the same activity they were doing when marked (the 'target activity'). Proportions were the number of marked ants engaged in the target activity, divided by the total number of that colour observed

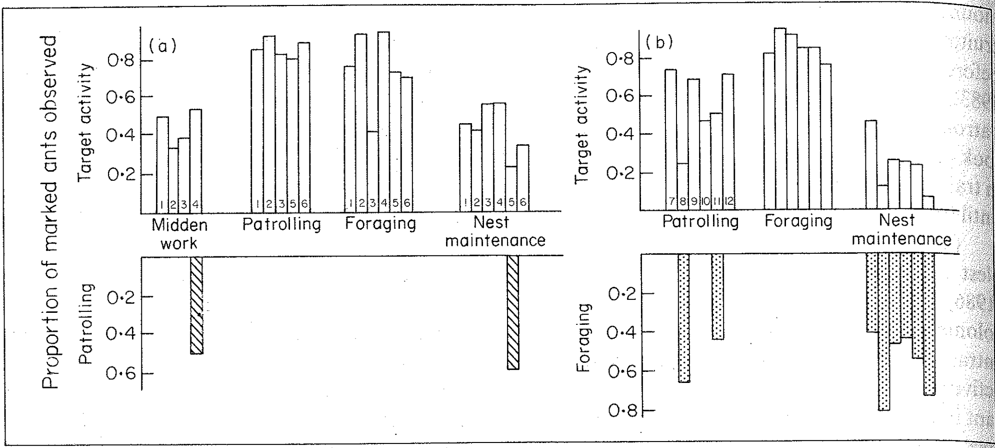

Figure 1. Task fidelity in undisturbed older (a) and younger (b) colonies. Upper half of each graph shows the proportions of marked ants that continue to do the target activity they were doing when marked; this activity is named for each cluster of bars. Lower half of each graph shows the proportions engaged in other activities. Numbers on bars identify colonies. In Figs 1–3, each vertical bar represents data from a single colony. If a colony was used in more than one experiment, a number identifying the colony is shown wherever data for that colony are represented. Thus figures with no labelled bars represent data from colonies used only in that experiment. Unless otherwise marked, bars for each colony are shown in the same order for every activity. If the number of bars shown differs between activities, bars are added to or deleted from the right-hand side of each activity cluster. Bars in the upper half of each graph show the proportions of marked ants observed to engage in the target activity. If more than 40% of the marked ants of one colony and activity engaged in any other activity besides the target one, a bar representing this second proportion is shown in the lower half of the graph, directly below the upper one representing the proportion in the target activity in the same colony. Thus if a vertically aligned upper and lower bar are shown for a given colony, they will sum to not more than 1. If the proportion indicated by the upper bar is small, but a lower bar is not shown, it means that marked ants did a variety of other activities besides the target activity.

that day in the course of 30–40 observations. For example, in undisturbed colony 3, on 1 August 1987, the proportion of marked nest maintenance workers that were observed to do nest maintenance was 79 out of 140, or 0·56 (Fig. 1a).

In most experiments, if ants switched tasks, ants marked in each of the four activities tended to switch into only one other activity. This is why most graphs in Figs 1–3 show proportions for only one activity, foraging or patrolling, in the lower half. If a total of fewer than 20 ants of a particular colour were seen on a given day, no proportions are shown for that colony and activity. This is why in some graphs, activities differ in the number of colonies for which data are shown. For example, in Fig. 1a, more than 20 marked foragers and nest maintenance workers were observed in each of six colonies. In colonies 5 and 6, fewer than 20 marked midden workers were observed, so, for these activities, data are shown for only four of the six colonies.

In undisturbed older colonies (Fig. 1a), ants marked as foragers continued to forage. Ants marked as nest maintenance workers continued to do nest maintenance, with the exception of one colony, in which a large proportion of marked nest maintenance workers did patrolling. Ants marked as patrollers continued to patrol. Ants marked as midden workers did either midden work or, in one colony, patrolling. This suggests that, in older colonies, there are distinct groups of exterior workers that engage in each of the four activities.

In undisturbed younger colonies (Fig. 1b), task fidelity is high only for foragers. Patrollers tended to continue patrolling, but they also foraged. Nest maintenance workers, however, were more likely to forage than to continue to do nest maintenance. If nest maintenance and foraging were interchangeable, a noticeable proportion of foragers would do nest maintenance work, but this was not the case. Instead, the results suggest that a distinct group of workers does nest maintenance but is likely to forage as well.

If ants did not specialize on any one task, ants of each colour would be later observed distributed randomly in each activity. To check this, a G-test of

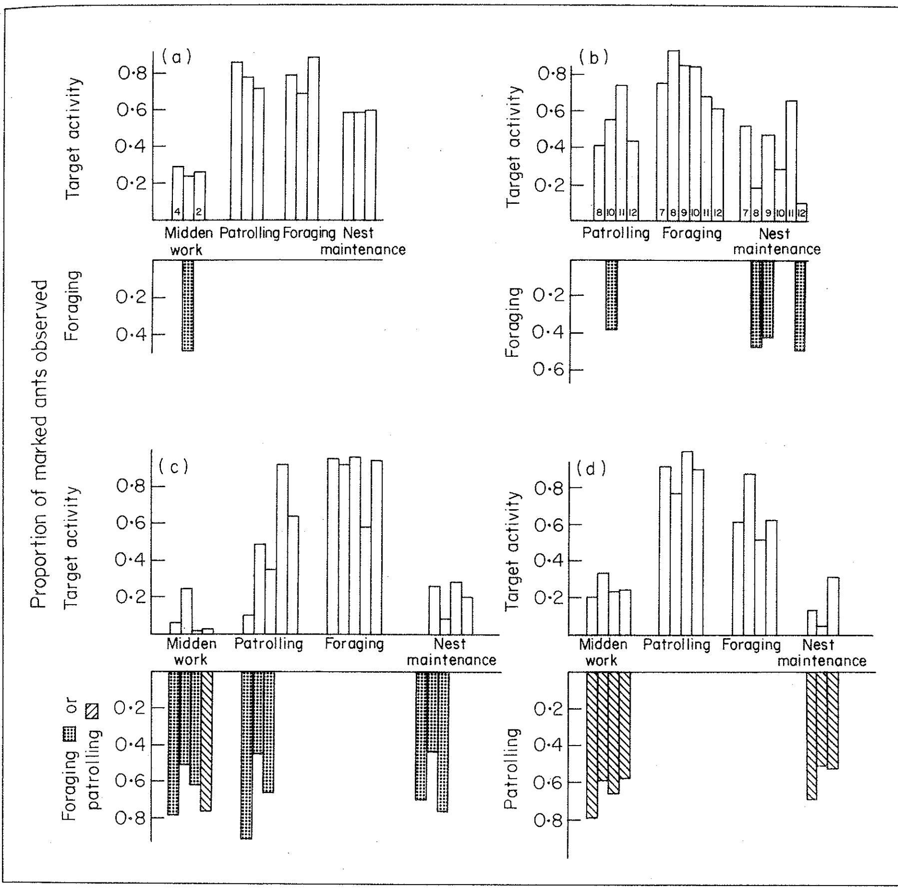

Figure 2. Task fidelity in response to perturbations. (a) Increased nest maintenance (older colonies); (b) increased nest maintenance (younger colonies); (c) increased foraging; (d) increased patrolling. Upper half of each graph shows the proportions of marked ants that continue to do the target activity they were doing when marked; this activity is named for each cluster of bars. Lower half of each graph shows the proportions engaged in other activities. Numbers on bars identify colonies. (See legend to Fig. 1 for details.)

heterogeneity was performed for data on undisturbed colonies, using the total numbers of ants engaged in each activity, counted in the course of 1 day of observations. In every colony, the test showed significant heterogeneity ($P<0{\cdot}05$; G-values ranged from 32·36 to 281·99, $df=9$, in older colonies, and from 8·85 to 88·18, $df=3$ since midden workers were not marked, in younger colonies). The observed distribution of marked ants into different activities was not random.

The perturbation experiments in which nest maintenance was intensified (Fig. 2a) suggest that, in older colonies, increased numbers of nest maintenance workers are due to ants recruited from inside the nest. The perturbations are known to increase numbers doing nest maintenance significantly (Gordon 1986, 1987), but workers engaged in other tasks did not tend to switch tasks to do nest maintenance. In the course of these experiments, marked nest maintenance workers were observed clearing away toothpicks. A final spurt of ordinary nest maintenance work, such as carrying sand out of the nest, was done later in the day by unmarked workers. Given that the numbers marked appear to be a large proportion of those engaged in nest maintenance, these observations suggest that the unmarked workers were previously inactive, newly recruited workers that completed the tasks unfinished earlier when regular, marked workers were busy clearing away toothpicks. In younger colonies

(Fig. 2b), marked nest maintenance workers in three out of six colonies switched tasks to do foraging, and in another colony, so did patrollers.

When numbers foraging were increased (Fig. 2c), high proportions of ants that were marked when engaged in patrolling, nest maintenance or midden work, all switched tasks to participate in the collection of a new, abundant food source. In one colony, marked nest maintenance workers primarily foraged to the exclusion of nest maintenance work.

When patrolling was experimentally intensified (Fig. 2d), high proportions of ants that were marked when engaged in nest maintenance switched tasks to patrol. Foragers did not switch tasks to join the increase in numbers patrolling. Some marked midden workers patrolled here (though in one undisturbed older colony midden workers patrolled anyway; Fig. 1a). Increased numbers patrolling in response to disturbance may include both extra patrollers that were previously inactive, and former nest maintenance workers that have switched to patrolling.

The results from experiments with marked 'extra' workers must be considered in the light of the results from perturbation experiments. In the case of intensified nest maintenance, extras were apparently recruited from a previously inactive pool. In the other perturbations, intensified foraging or patrolling, marked ants switched task. When experiments with marked extras were done using the latter perturbations, these extras probably included ants that had switched from other tasks.

When ants were recruited, presumably from all three other tasks (Fig. 2c) to act as extra foragers, they either continued foraging or patrolled (Fig. 3a, b).

Once ants were recruited into patrolling, (Fig. 3c, d), both from the ranks of nest maintenance workers and possibly also from inside the nest, they tended to continue patrolling. Extra patrollers did not switch to do nest maintenance work (Fig. 3c), even when nest maintenance was experimentally intensified. When numbers foraging were increased (Fig. 3d), extra patrollers in only one of three colonies switched to foraging.

Perturbations in which nest maintenance was intensified suggested that extra nest maintenance workers are recruited from previously inactive ants inside the nest (Fig. 2a). The experiments in which these extras were marked (Fig. 3e, f) showed that they, like regular nest maintenance workers, had very low task fidelity. When patrolling was experimentally intensified (Fig. 3e), both regular and extra nest maintenance workers tended to patrol. When foraging was experimentally intensified (Fig. 3f), both regular and extra nest maintenance workers tended either to forage or to patrol.

The results are summarized in Fig. 4. Foragers showed very strong task fidelity. In undisturbed colonies, and in response to perturbations, ants marked when foraging continued to forage. Ants recruited from other tasks to do extra foraging, tended to continue foraging. In contrast, nest maintenance workers showed very weak task fidelity. In response to perturbations causing increases in patrolling or foraging, nest maintenance workers often switched to one of these tasks. Experiments that increased numbers doing nest maintenance drew extra workers from within the nest, but later these extra workers often did some other task. Patrollers showed an intermediate task fidelity. They continued patrolling unless more foragers were required, and tended not to do nest maintenance.

DISCUSSION

In undisturbed colonies, there appear to be four distinct groups of exterior workers: foragers, nest maintenance workers, patrollers and midden workers. Other *Pogonomyrmex* species have similar groups of exterior workers (e.g. Gordon 1984b for *P. badius*; Porter & Jorgensen 1981 for *P. owyheei*).

The perturbation experiments show that when more ants are required for particular tasks, some workers change tasks. The probability of task switching, and the tendency to remain in a new task once a worker has switched, both vary among the different groups of exterior workers.

In interpreting the results of this study, I make two assumptions. (1) The effects of perturbation experiments on the numbers of ants in various activities were, as they appeared to be, the same as the effects of previous experiments (Gordon 1986, 1987). Previous effects were similar in repeated experiments using about 40 older and 30 younger colonies in the course of two summers; there is no reason to think they should be different in subsequent summers. (2) I repeated each perturbation experiment in several colonies, and each experi-

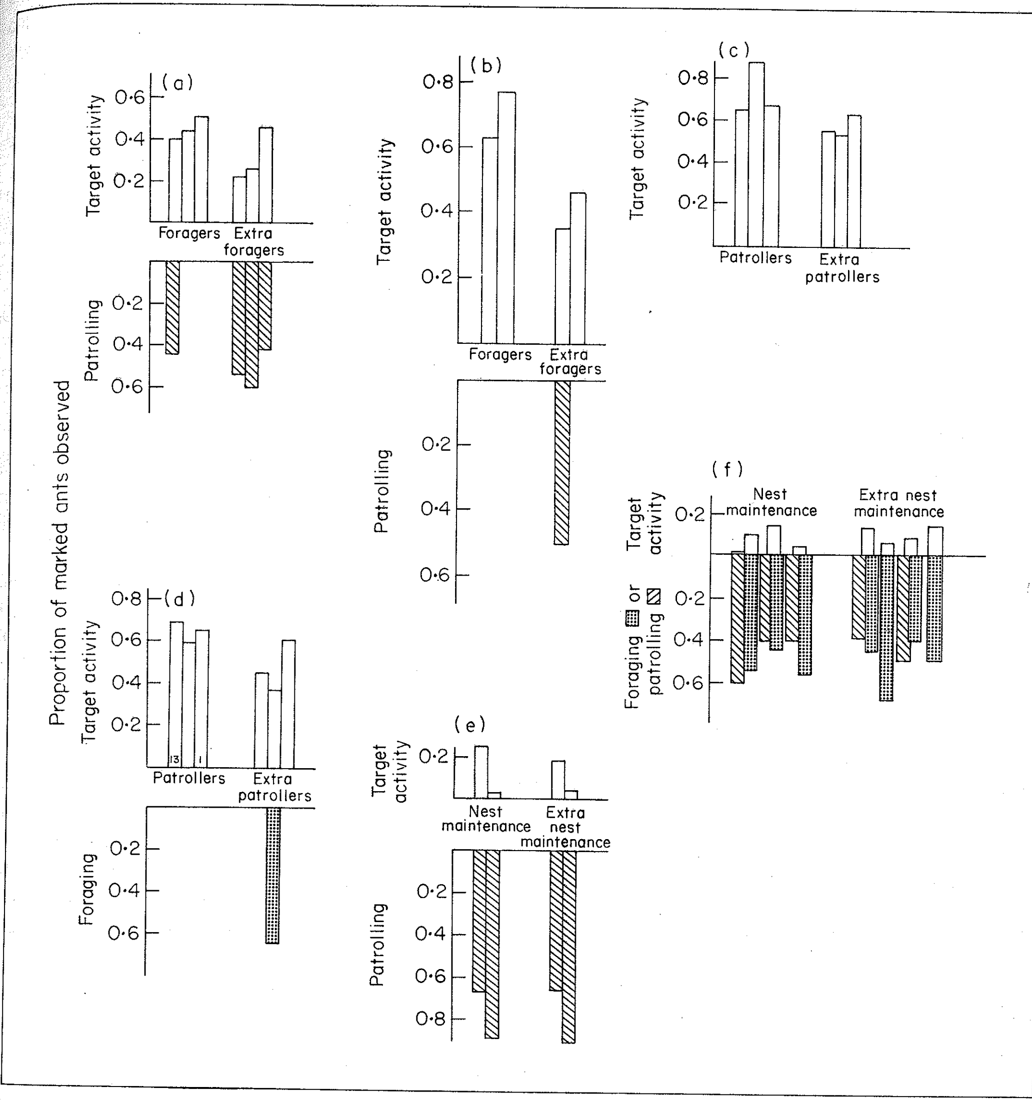

Figure 3. Task fidelity of extra workers. (a) Extra foragers: increased nest maintenance; (b) extra foragers: increased patrolling; (c) extra patrollers: increased nest maintenance; (d) extra patrollers: increased foraging; (e) extra nest maintenance: increased patrolling; (f) extra nest maintenance: increased foraging. Upper half of each graph shows the proportions of marked ants that continue to do the target activity they were doing when marked; this activity is named for each cluster of bars. Lower half of each graph shows the proportions engaged in other activities. Numbers on bars identify colonies. (See legend to Fig. 1 for details.)

ment with marked extras in at least two colonies. I assume it to be unlikely that, in many colonies, the distributions of large samples of marked ants would show similar trends, consistent across experiments, which mask different, hidden trends in the distribution of unmarked ants.

In the allocation of harvester workers to various tasks, it seems that ants are drawn into foraging and away from nest maintenance (Fig. 4). This may explain why, in previous removal experiments, the nest maintenance workers and foragers that replaced removed workers appeared to be derived from a common pool (Gordon 1986). In other ant genera, nest maintenance workers seem to act as a

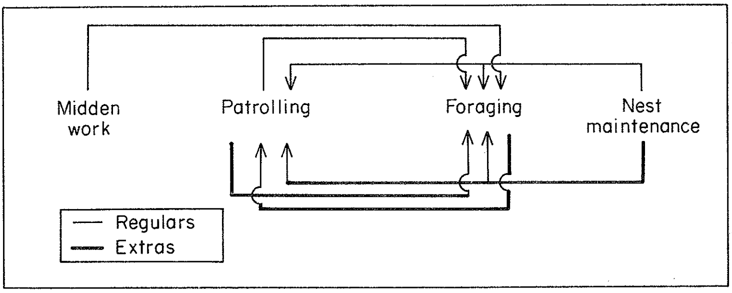

Figure 4. Task switching in response to perturbations. For each activity, arrows show which other activities regular and extra workers in perturbed colonies will do.

pool of reserve foragers (Weir 1958; Lenoir 1979a). Data on worker longevity in *P. barbatus* (Gordon & Holldobler 1988) suggest that nest maintenance workers have a longer life expectancy than either foragers or patrollers. If *P. barbatus* follows the sequence of age-dependent changes of task that is usual in ants, nest maintenance workers may be the youngest group of exterior workers, in transition from interior to exterior tasks. This may explain why nest maintenance workers are so much more likely to switch out of nest maintenance work than back into it. Once they have taken on one of the other, more fully exterior tasks, new nest maintenance workers can be drawn from the pool of younger ants inside the nest.

The results of Porter & Jorgensen (1981) suggest that the dynamics of worker variability in *P. owyheei* are similar to those of *P. barbatus*. They defined exterior activities differently, but I take their 'refuse workers', ants carrying things out of the nest, to be similar to nest maintenance workers; foragers to be the same as foragers defined here; and their 'defenders' to overlap with the patrollers described here (though 'defenders' were those ants that came out of the nest in response to an experimentally induced disturbance, and thus include extra patrollers as defined here, which may have switched from other tasks; Fig. 2d). They found that 'refuse workers' later became foragers, but foragers and defenders rarely did nest maintenance work.

It is interesting that workers in the most labile category, nest maintenance, differ most in task fidelity when older and younger colonies are compared. In other species, individuals show more task flexibility in younger colonies (Lenoir 1979b). It may be that, as the colony matures, changes in the allocation of workers to nest maintenance contribute to the increasingly consistent behaviour of older colonies.

Perturbations causing increased numbers doing nest maintenance work also caused a decrease in numbers foraging (Gordon 1986, 1987). In the present study, foragers rarely switched tasks to do nest maintenance when nest maintenance was experimentally intensified (Fig. 2a). Thus it appears that task switching does not account for the decrease in numbers foraging. Mechanical obstruction of the nest does not account for this either, and nest maintenance and foraging go on at different times of day. What keeps the foragers inside the nest? The decrease in foraging must be the result of a communication system which signals foragers about the status of nest maintenance work. Similarly, previous experiments in which numbers patrolling were increased showed significant decreases in numbers foraging, relative to undisturbed colonies (Gordon 1987). In the present study, marked foragers rarely switched tasks to do patrolling when numbers patrolling were increased (Fig. 2d). Again, the colony-level result, decreased numbers of foragers, cannot be explained as the result of task switching by foragers.

The results suggest that the task of an individual worker is affected by the recent history of the colony's requirements. This would account for equivocal results on the tendency of patrollers to switch to foraging. When numbers foraging were experimentally increased, high proportions of regular patrollers were observed to forage (Fig. 2c). But when foraging was intensified the day after patrolling had been intensified in order to mark extra patrollers, regular patrollers in three other colonies did not forage (Fig. 3d). Patrollers may show higher task fidelity the day after a disturbance has increased colony needs for patrollers, than they do when extra food is given to a previously undisturbed colony.

Many studies have demonstrated task fidelity in various ant species. There have been relatively few investigations of task switching, and many of these examine how colonies maintain constant numbers in various tasks in response to removal of workers (e.g. Wilson 1983, 1984; Sörensen et al. 1985). Here, I consider a different problem: how task switching contributes to changes in worker allocation when a colony's environment is altered. The results show that colony response to changing environments includes a complex dynamics of task switching.

What a colony does in a particular situation depends not only on how many individuals of each type are available to do each task, but also on how the global state of the colony affects the behaviour of individuals. As Oster & Wilson (1978) pointed out, natural selection acts on variation among colonies in their behaviour. Colony behaviour is dynamic, governed by rules that determine the extent to which, in changing conditions, a colony will forage, maintain and enlarge its territory, and, ultimately, reproduce. To understand how social insect colonies evolve, we need to learn more about these dynamics. This requires further research on how individuals change tasks, and how colonies change the allocation of effort to different tasks, in changing environments.

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