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Group-level dynamics in harvester ants: young colonies and the role of patrolling

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Abstract. The flexibility of colony organization in the red harvester ant, *Pogonomyrmex barbatus,* was investigated in the field in older (about 5 years) and younger (about 2 years) colonies. Perturbations affecting nest maintenance work, foraging and patrolling were made singly and in various combinations. In both younger and older colonies, events that directly affected only one activity caused changes in the numbers of ants engaged in other activities. An increase in patrolling early in the activity period caused foraging to decrease later on. Combined perturbations show that in both younger and older colonies, all three activities were linked by complex, synergistic interactions: the response to a perturbation affecting one activity itself varied, depending on the states of the other activities. The results suggest a more strongly homeostatic response to perturbations in older colonies than in younger ones: older colonies appeared to respond more consistently to single perturbations, and to decrease foraging less in combined perturbations, than did younger ones. Individual workers live only about a year. Thus similarities and differences in the flexibilities of colonies 3 or more years apart are organizational rather than a result of the accumulated experience of particular individuals. Ontogenetic changes in a colony's response to environmental stress may be ecologically important.

The harvester ant, *Pogonomyrmex barbatus,* lives in desert communities containing many other species of harvester ants, as well as rodents, all of which eat the seeds of annual plants. Food is a limiting resource for various species competing, in the ecological sense, in many subtle ways (Davidson 1985). The social behaviour underlying the ecological structure of desert communities is poorly understood. From the perspective of an ant colony, the ecologically relevant social behaviour is the colony's response to environmental events. How do changes in food supply, intrusions by other ants, alterations to nest structure caused by wind, rain and other animals, all affect colony behaviour?

In the daily round of a harvester ant colony, various tasks are performed outside the nest by groups of ants. Such tasks include foraging, patrolling, nest maintenance work and the sorting and upkeep of the colony's midden, which is comprised of piles of seed husks and a layer of pebbles covering the mound. The daily round, consisting of temporal and spatial patterns in these activities, is the manifestation of the colony's day-to-day interaction with its environment. On some days, for example, nest maintenance activity prevails, while on others, most ants active outside the nest are foraging. The dynamics of the daily round are the rules for how it changes as the colony's environment changes.

The present study continues an investigation of the dynamics of the daily round. In a previous study (Gordon 1986), I found that separate perturbations affecting the temporal patterns in either nest maintenance or foraging each caused changes in the temporal patterns of other activities. Perturbations affecting nest maintenance and foraging simultaneously, led to a synergistic or non-additive effect. That is, combined perturbations showed a complex interaction between the two activities. Colony response to a perturbation of nest maintenance depended on the state of foraging, and vice versa.

The present study extends this work in two ways, posing the following questions.

(1) How does patrolling affect the dynamics of the numbers engaged in different tasks? Patrollers monitor the colony environment near the mound, and probably along the foraging trails as well. They react to novelty, disturbance and new food sources. Most patrolling is done early in the morning activity period, when neighbouring, less heat-

tolerant ant species are active (Bernstein 1979), and when the colony seems to set its course for the day's foraging (Gordon 1983). Will perturbations that directly affect only the early morning patrollers cause later changes in the numbers of workers doing other tasks? How will the level of disturbance affect the intensity of foraging? Are connections among other tasks modulated by events affecting patrolling; that is, will combined perturbations involving patrolling show non-additive effects?

(2) Previous experiments were done with established colonies at least 5 years old. There are far more young colonies than older, well-established ones. Mortality of young colonies is very high (Wilson 1971), presumably as a result of competition for food between sympatric harvester ant species and granivorous rodents. *P. barbatus* colonies seem to become established, and their growth rates begin to level off, at about 5 years of age (personal observation). I did perturbation experiments using colonies about 2 years old, probably containing only one-fifth as many ants as the older colonies (MacKay 1981; Markl & Holldobler, personal communication). Although it seems to be generally true of most ant species that the distribution of workers of different age and/or size classes changes as a colony matures (Oster & Wilson 1978), we know little about ontogenetic changes in a colony's response to environmental events.

Colonies 3 years apart in age are very different, both in worker numbers and in ecological role. These differences might be reflected in the complexity of colony organization. Are different activities already inter-dependent in 2-year-old colonies, and in what ways? Do events affecting one activity change the numbers of workers engaged in other tasks? If so, are numerical relations between activities modulated by the extent of environmental stress? That is, will combined perturbations lead to non-additive effects in younger colonies?

METHODS

Field experiments were conducted in southeast Arizona in a mesquite-chaparral habitat, near the Southwestern Research Station, from 1 July to 10 August 1985.

Experiments were done using a group of 37 older colonies and another group of 35 younger ones. Older colonies contain more ants (MacKay 1981). As a colony grows, it clears a larger nest mound, builds longer and wider foraging trails, establishes a larger, more distinct midden of cleared bits of vegetation and seed husks, and brings in more pebbles to cover the mound.

The selection of the colonies to be used in the experiments was based on the following measures of nest size: cleared area (measured as the distance between the closest two bushes straddling the nest entrance), area covered with pebbles, and width of the cleared foraging trails. Using a procedure similar to that of Jonkman (1980), I estimated a colony's age by comparing measures of its nest size with those of colonies that already had large, well-established nests in 1981, and which were thus at least 5 years old. Based on these comparisons, I estimate that the older colonies used here were between 5 and 10 years of age. Based on observations of the nests of younger colonies from 1981–1985 (most of which disappeared from one summer to the next), the younger colonies I used were estimated to be about 2 years old. The mean cleared distance for older colonies was 137·4 cm, for young colonies, 66·3 cm; the mean width of the foraging trail for older colonies was 9·4 cm, for young colonies, 6·9 cm. In both measures, the means depended significantly on age (*t*-test, $P < 0{\cdot}001$).

Perturbations

Three types of perturbations were made. Nest maintenance activity was increased by placing a pile of toothpicks near the nest entrance, which nest maintenance workers carried to the edges of the nest mound and then ignored. The numbers of ants foraging were decreased by placing plastic barriers on the foraging trails that the ants could only bypass with some difficulty. (See Gordon 1986, for a full description of these two perturbations.)

To examine a third activity, patrolling, I introduced a third perturbation, consisting of two simultaneous manipulations, referred to jointly as 'commotion'. First, alien ants, *Novomessor cockerelli,* were collected with an aspirator and released on the *P. barbatus* nest mound near the nest entrance, at the beginning of the activity period when patrollers were first emerging. The *Novomessor* circled around, were chased by *P. barbatus* workers, and were always gone within the hour. *Novomessor* is active at night, and while ants do occasionally venture onto harvester ant mounds in the early morning, they are usually back in their own nest by the time harvester ant activity reaches its peak in mid-morning. At the same time, further patrolling was elicited using a small cardboard cylinder (5 cm in length, 4·5 cm in diameter), attached by a thin wire to a heavier wire stake 7·5 cm high. The wire stake was put into the nest mound near the nest entrance, taking care not to go deep enough to cave in any nest chambers. One edge of the cylinder rested on the nest entrance and moved around slightly in the wind. The patrollers inspected it, crawled on it, and eventually, since it could not be moved, ignored it. It thus constituted an alien object, only temporarily disturbing. Both forms of interference with patrolling, alien ants and cardboard cylinders, were done when patrollers were first emerging. The response died down before most activities were under way, though nest maintenance had usually begun before the patrollers' inspection of the cylinders had subsided.

Because younger colonies were smaller than older ones, they were subjected to perturbations on a smaller scale, as follows: older colonies, 200 toothpicks; younger colonies, 150 toothpicks; older colonies, 10 *Novomessor* and two cylinders; younger colonies 5–7 *Novomessor* and two cylinders; older colonies four barriers; younger colonies usually two barriers, or four if two foraging trails were present. These adjustments in the scale of perturbations for younger colonies were based on pilot experiments to determine how much a younger colony would tolerate without drastic alterations in its behaviour, such as the cessation of activity outside the nest.

Experimental Design

Perturbations were made in various combinations as shown in Table I. Each experiment, which lasted 3–7 days, was made using either older (O) or younger (Y) colonies. In each experiment, one group of colonies was left undisturbed as controls, while each other group of colonies received a particular perturbation. Each line of Table I shows the perturbations that were made concurrently, every day, during the course of one experiment.

During the course of a given experiment, each colony was observed once each hour throughout the morning activity period, from 0500 through 1100 hours. The number of observations for each experiment (Table I) is thus the product of the numbers of days, treatments, colonies per treatment, and h per day (always 6), minus the number of missing observations. An observation consisted of recording the numbers of ants engaged in each activity within 0·3 m of the nest mound's edge (see Gordon 1986 for details): nest maintenance workers carry sand out of the nest and clear vegetation at the edges of the nest mound; foragers travel directly away from or towards the nest on the foraging trail; patrollers move with a characteristic zig-zag, hesitant gait, inspecting the ground or other ants frequently, or gather at the site of a disturbance and stand with mandibles open; midden workers bring objects to the midden and rearrange it. Because it took longer (about 1 min) to count ants in the larger, older colonies, observations were made once for each older colony every 65 min instead of each 60 min, and observations lasted until 1130 hours.

The actual order of experiments was: Y1, x, Y2, Y3, x, Y4, x, O3, O2, O4, O1, where 'x' indicates a day elapsed between experiments. The order of the experiments was changed for O1–O4 for incidental reasons. After each experiment (within an age group), the colonies from all treatment groups, including controls, were each assigned randomly to another treatment group. Thus each colony received various treatments, and sequences differed for each colony. The differences in sequence, and the large numbers of colonies would, it was hoped, balance out the effects of sequence on particular colonies across the 30 colonies in each age group. The time required to recover from perturbations was not known, though in previous experiments colonies receiving toothpicks and barriers for 6 days still showed altered daily rounds during the succeeding week in which no perturbations were made (Gordon 1986).

Data Analysis

To normalize for differences in colony size, for each colony I found the largest total number of workers ever counted in any single observation, and used it as a measure of the size of the exterior worker force of that colony. All data for that colony were converted to proportions of this largest total.

Previous experiments done in 1984 showed that the response to perturbation changed from week to week. For this reason, the design consists of a series of short experiments (3 – 7 days) to minimize day-to-day effects within experiments. Each experiment was analysed separately, using a four-way, full factorial ANOVA (BMDP P4V), with day (1 – 7 in Y1, otherwise 1 – 3), treatment (controls and three

Table I. The experimental design

				Treatments							
Experiment*	Days	Colonies per treatment	Number of observations	Controls	Toothpicks (TP)	Barriers (B)	Commotion (C)	TP+B	TP+C	B+C	TP+B+C
Y1	7	5	840	X	X	X		X			
O1	3	7	497	X	X	X		X			
Y2	3	7	483	X	X		X		X		
O2	3	7	503	X	X		X		X		
Y3	3	7	500	X		X	X			X	
O3	3	7	504	X		X	X			X	
Y4	3	6	540	X	X	X	X				X
O4	3	6	526	X	X	X	X				X

Age of experimental colonies (old or young) is designated by 'O' or 'Y'.

Table II. Summary of ANOVA results

					Interaction									
Experiment†	Day (D)	Treatment (T)	Activity (A)	Hour (H)	DT	DA	DH	TA	TH	AH	DTA	DTH	DAH	TAH
Y1	*	*	*	*	*	*	*	*	*	*				
Y2	*	*	*	*		*	*	*	*	*			*	
Y3		*	*	*		*	*	*		*			*	
Y4	*	*	*	*		*	*	(0·005)	*	*				
O1	*	*	*	*		*	*	*	*	*				
O2	*	*	*	*		*	*	*		*			*	
O3	*	*	*	*	*	*	*	*		*	*		*	
O4	*	*	*	*	*	*	*	*	*	*			*	

* Indicates $P<0{\cdot}001$.

† Age of experimental colonies (old or young) is designated by 'O' or 'Y'.

Table III. Mean normalized numbers of ants in each activity in undisturbed colonies (controls)

Experiment*	Midden work	Patrolling	Foraging	Nest maintenance
Y1	0·0002	0·0092	0·0959	0·0234
†Y2	0·0009	0·0463	0·3171	0·0535
†Y3	0·0034	0·0442	0·2310	0·0755
Y4	0·0023	0·0312	0·0651	0·0368
O1	0·0063	0·0356	0·0988	0·0723
†O2	0·0009	0·0574	0·2006	0·0647
†O3	0·0011	0·0629	0·3233	0·0683
O4	0·0016	0·0524	0·1314	0·0939

* Age of experimental colonies (old or young) is designated by 'O' or 'Y'.

† Indicates heavy rains (at night) during the experiment.

or four perturbations), activity (nest maintenance, foraging, patrolling and midden work) and hour (0500 through 1100 hours) as main effects, and arcsine transformations of the normalized number of ants as the dependent variable. Effects were considered significant at $P < 0{\cdot}001$. In some hours, no ants were observed engaging in a particular activity, which led to heterogeneous variances and thus a conservative choice of significance level.

RESULTS

Perturbations had significant effects, not only upon activities interfered with directly, but upon various other activities as well (Table II; full ANOVA tables are available from the author). The significant treatment effects in all the experiments (Table II) show that counts in perturbed colonies differed from those in controls. The significant treatment by activity interactions in all the experiments show that changes in various activities differed according to treatment. These results confirm and extend those reported previously (Gordon 1986) for an experiment similar to O1, done here with a larger number of colonies per treatment. The new perturbation, affecting patrolling, caused significant changes in the daily round (experiments Y2–Y4, O2–O4).

As in previous studies, the daily round, or temporal patterns in the numbers of workers engaged in each activity, led to significant effects of activity, hour, and activity × hour interactions in all experiments (Table II). The daily round varies from one day to the next, probably because of environmental factors such as changes in weather (significant day effects, and day × hour and day × activity interactions, Table II).

The effects of various treatments on the numbers of ants in each activity are shown in Figs 1 – 4. Each figure represents the results of one experiment. For each perturbation, the figure shows the difference between the mean number of ants observed in a given activity, and the same mean in control colonies. (Control means are shown in Table III.) These differences are further corrected for the overall mean, across activities, for each perturbation. That is, if a perturbation caused all activities to decrease, for example, this decrease is added to all differences from control means. Each point thus represents the deviation from controls in a particular treatment and activity. The dotted line shows the hypothetical additive effects of all single perturbations, obtained by summing the corrected mean differences for each activity over all single perturbations in a given experiment.

If perturbations had no effect, and colonies receiving perturbations were similar to undisturbed control colonies, the means for perturbed activities would all be close to the zero line. If changes in one activity had no effect on other activities, results for activities not perturbed would also lie near the zero line. If colonies responded in only one way to a particular perturbation, results from the combined perturbations would match the lines showing the hypothetical additive effects. Instead, the figures

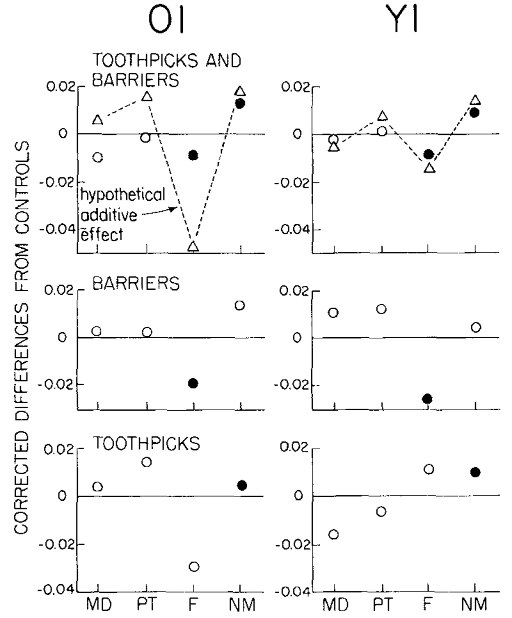

Figure 1. Effect of perturbations on each activity: perturbations of nest maintenance, foraging and both. Each point represents the difference between the control group and the treatment group, in mean normalized numbers of ants engaged in an activity. In each perturbation some differences were significantly greater than zero (see text and Table II for details). Differences are corrected for overall treatment effects as explained in the text. Corrected differences for activities receiving perturbations are shown with closed circles; differences for other activities are shown with open circles. Open triangles connected by a dotted line on graphs for combined perturbations show the hypothetical additive effect obtained by summing the differences from controls resulting from single perturbations. MD = midden work; PT = patrolling; F = foraging; NM = nest maintenance; older colonies = O1; younger colonies = Y1.

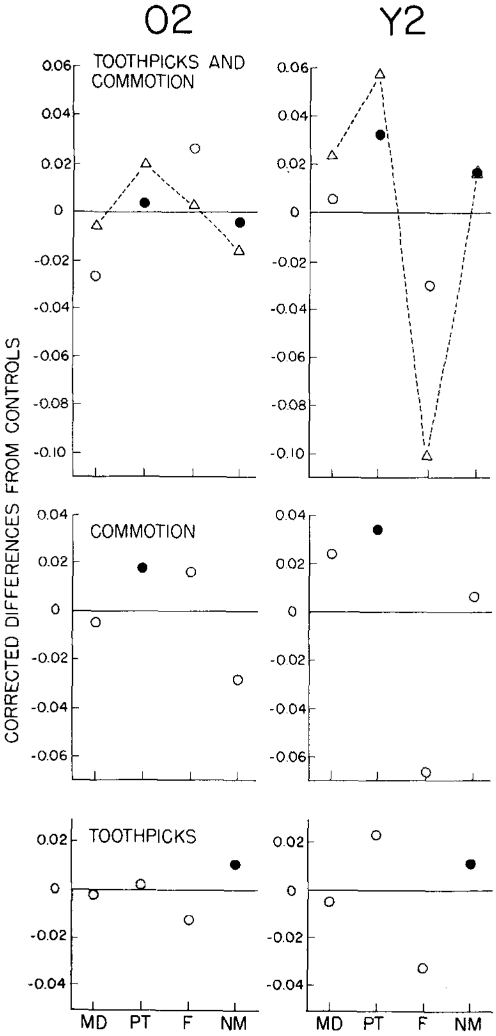

Figure 2. Effect of perturbations on each activity: perturbations of nest maintenance, patrolling and both. See legend for Fig. 1. Older colonies = O2; younger colonies = Y2.

show that perturbations changed both the activities directly affected by experiments, and other activities as well. In most of the experiments (except O3), the responses to combined perturbations show non-additive effects. In both younger and older colonies, patrolling, nest maintenance and foraging are linked so that the response to a perturbation of one activity depends on the states of the other two activities. The significant treatment × activity interactions in each experiment confirm that at least some of the deviations from controls shown in each figure are significantly different from zero.

In both younger and older colonies, perturbations affecting patrolling, or commotion, clearly caused an increase in patrolling, as expected (Figs 2–4). Commotion also caused mean numbers in other activities to deviate from the controls. This shows that the behaviour of other worker groups is contingent on the amount of patrolling being done, as it is on the amounts of nest maintenance and foraging. Except in O2, the effect of commotion as a single perturbation is always to decrease foraging, as well as to increase patrolling. In general, in both age groups, single perturbations caused foraging to decrease and patrolling to increase.

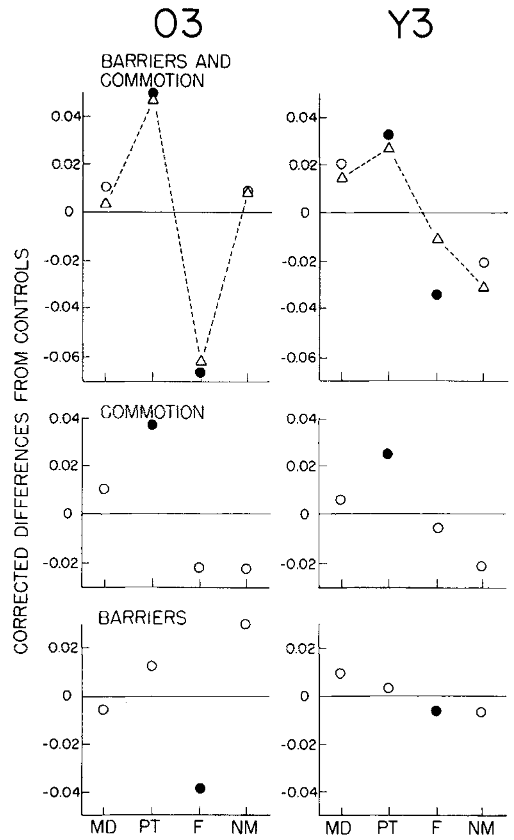

Figure 3. Effect of perturbations on each activity: perturbations of foraging, patrolling and both. See legend for Fig. 1. Older colonies = O3; younger colonies = Y3.

A comparison of the results across separate experiments suggests there may be age differences in colony response to perturbations. As in previous experiments, day effects were always significant (Table II). To obtain concurrent observations in each experiment from as large a number of colonies as possible, experiments on younger and older colonies were done at different times. In the present design, age and day are totally confounded. Thus it is not possible to make any statistical claims about the magnitude of age differences. However, in four pairs of separate experiments, older and younger colonies differ in consistent ways.

Across the same perturbations in successive experiments, the response of older colonies appears to be more consistent than that of younger colonies (Fig. 5). Comparing the curves for older colonies receiving toothpicks in O1, O2 and O4, one finds that the older colonies' reactions were similar across experiments; the curves are of similar shape. Again, the three curves for barriers in older colonies are of similar shape, except for variation in changes in midden work relative to patrolling. Analogous curves for younger colonies receiving toothpicks or barriers are not as similar. In younger colonies, relative changes in each activity differed more across the three experiments than they did in older colonies. The response to commotion, however, is similar in both age groups, especially in O2,

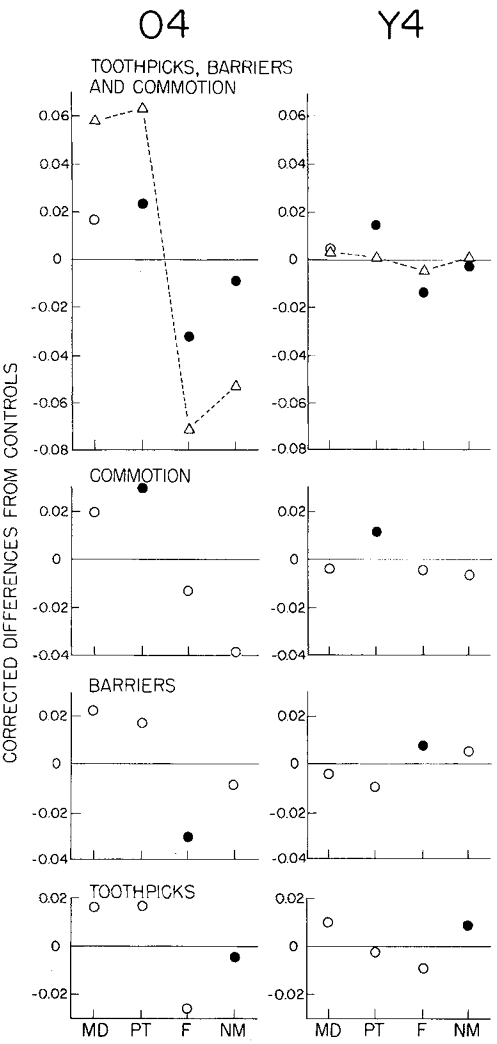

Figure 4. Effect of perturbations on each activity: perturbations of foraging, nest maintenance, patrolling and all three. See legend for Fig. 1. Older colonies = O4; younger colonies = Y4.

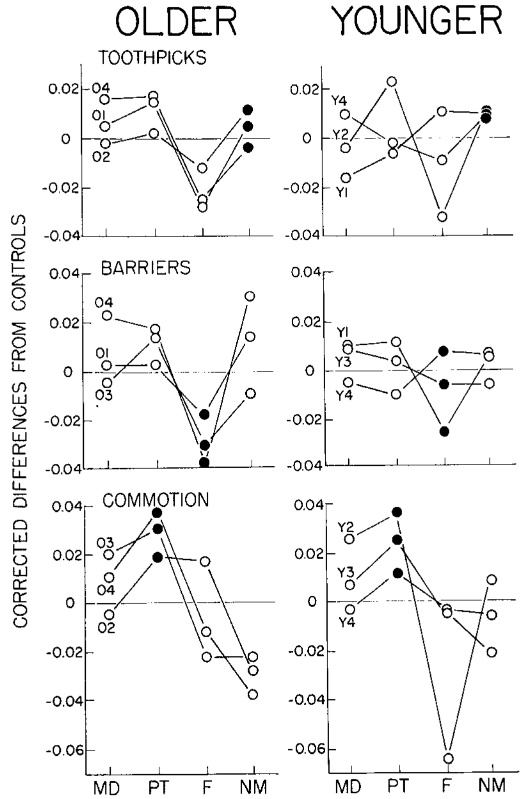

Figure 5. Age differences in the consistency of response to single perturbations. Each point represents the corrected difference from controls, exactly as in Figs 1 – 4. In this figure the results from the same perturbation, in successive experiments, are shown together. Corrected differences from controls for activities receiving perturbations are shown with closed circles; those for other activities are shown with open circles. MD = midden work; PT = patrolling; F = foraging; NM = nest maintenance.

O4, Y3 and Y4. Once in each age group (O3 and Y2), deviations from controls in nest maintenance are different from the other two commotion perturbations.

To explore whether younger colonies differ more from one another than older colonies do, I looked at the variances across colonies within experiments, in the two age groups. The variances appear to be remarkably similar; within an experiment, younger colonies seem to resemble one another as much as older colonies resemble one another. But Fig. 5 shows that distinct groups of younger colonies, in successive experiments, differ more from one another than older groups do. This suggests that younger colonies are more affected by week-to-week changes in environmental conditions, across successive experiments, than older colonies are.

Older and younger colonies also seem to differ in their responses to combined perturbations. In all of the experiments, response to combined perturbations differs from the additive effects of the single perturbations. (In O3, however, the non-additive effect is negligible; see Fig. 3.) Synergistic effects on the numbers of workers foraging differ consistently across age groups (combined perturbations, Figs 1–4). In older colonies, the response is a more strongly homeostatic one; in combined perturbations, older colonies are closer to controls in the numbers of workers foraging. Younger colonies decrease foraging more when subjected to the increased stress of combined perturbations. In all of the experiments, the older colonies' response to combined perturbations, relative to hypothetical additive effects, was to decrease foraging less than the younger colonies did. In the same situations, younger colonies decreased foraging more (Y2–Y4), or did not increase it as much as older ones (Y1).

In older colonies, the relationship between nest maintenance and foraging is more strongly reciprocal than it is in younger colonies. In older colonies, a reciprocal relationship seems to hold in all perturbations, except for commotion in O3. In younger colonies, reciprocity between nest maintenance and foraging is weaker, especially in Y1 toothpicks, Y3 barriers, Y4 commotion and Y4 barriers. A weaker reciprocal relationship between nest maintenance and foraging in younger colonies also emerges in the effects of weather changes on the undisturbed control colonies in each age group (Table III). In rainy weather, foraging increases in both age groups. (Rain may uncover new supplies of fallen seeds previously buried in the sand, D. Davidson, personal communication.) In older colonies, increased foraging in rainy weather is accompanied by decreased nest maintenance; in younger colonies, both nest maintenance and foraging increase.

DISCUSSION

The results raise intriguing questions about the mechanisms regulating, on a moment-to-moment basis, the numbers of ants engaged in each task. Ants doing a certain task apparently monitor their own numbers and the numbers doing other tasks, perhaps by means of other ants inside the nest acting as a central source of information. Do ants keep track of the numbers doing a task or the amount of the task that is accomplished? Seeley (1986) found that in honey bees, the numbers foraging are modulated by the availability of nectar. The present work raises a further question: in what way is the status of one task communicated to workers doing another task?

However individuals may obtain information about other tasks, the way that they respond to this information is also not known. One salient question is, do the ants that are already active switch tasks, or are others recruited into various activities from inside the nest? The size of the exterior work force of a *Pogonomyrmex* colony is only about 10–20% of that of the colony (reviewed in MacKay 1981). Some workers inside the nest are occupied with brood care, food storage and nest maintenance. The rest of the colony seems to constitute a large reserve pool inside the nest. There is evidence that at least some of the changes observed here are caused by recruitment from workers inside the nest. The total numbers of active workers do not appear to be the same in colonies receiving different perturbations, as they would if only switching were taking place, in a zero-sum allocation of workers. Previous experiments in which workers were removed also suggest recruitment of interior workers in response to perturbations (Gordon 1986). The existence of non-additive effects in combined perturbations demonstrates that a particular perturbation does not simply cause a particular exchange of tasks between a pair of activities.

However, the possibility that workers are switching tasks cannot be ruled out. In two other *Pogonomyrmex* species, experiments with marked individuals in undisturbed colonies show that different activities are done by distinct groups, and that an individual's task changes as it gets older (Porter & Jorgensen 1981; Gordon 1984). However, there is growing evidence that though individual ants tend to do only certain tasks, they will change tasks in response to environmental events (Meudec & Lenoir 1982) or to the removal of workers of a certain type (Wilson 1984). The present results provide some evidence that switching is taking place in response to perturbations. Younger colonies probably have a smaller reserve pool than older ones; this assumes that the size of the reserve pool is determined relative to colony size, and that the curve of colony growth is sigmoid (Oster & Wilson 1978). If recruitment were solely responsible for the relationship between nest maintenance and foraging, younger colonies should show a stronger reciprocal relation than older colonies with larger reserves. The opposite is the case: older colonies, with larger pools of reserves, show a stronger reciprocal relation between nest maintenance and foraging. Experiments with marked individuals are being planned to investigate how the relative magnitudes of switching and recruitment are modulated by various kinds of environmental change.

Whatever the mechanisms at the individual level, worker numbers in various activities are clearly regulated in response to environmental events. The results suggest that this regulatory process may change as the colony matures. It seems unlikely that the age differences noted here could arise from coincidental day effects, presumably due to weather, of the eight groups of days chosen for the experiments. It should be kept in mind that the age differences in colony flexibility suggested by these results are differences in colony organization. They are related to colony age, not differences in the ages of individual workers. Individual workers in other *Pogonomyrmex* species live for about a year in the laboratory (Porter & Tschinkel 1982), or less in the field (Porter & Jorgensen 1981). Behavioural differences in colonies 3 or more years apart in age do not arise from experience that particular individuals have accumulated throughout those 3 or more years.

What changes in organization take place as an ant colony matures? Most of what we know about the ontogeny of ant colonies concerns their demography rather than behaviour. The relevant work has been based on the premise that ants of a given age/size class do particular tasks (e.g. Wilson 1985). Empirical studies have documented changes in colony ontogeny in the distribution of age/size classes (Wilson 1983); theoretical work has led to predictions about ontogenetic changes in colony demography (Oster & Wilson 1978). In any ant colony, the founding queen lays eggs that hatch into workers who begin to function as a colony. As *P. barbatus* colonies get older, the number of ants increases, and the distribution of ants in each age class, available to do various tasks, almost certainly changes as well. One way to begin examining how colony organization develops is to separate the effects of colony age and size (Wilson 1983).

Experiments are being planned to test whether age differences in daily round flexibility depend on colony size.

It is becoming clear that demographic counts of the numbers of individuals available in each age/size class are not sufficient to predict the behaviour of a colony. If this is true, the ontogeny of colony organization cannot be fully characterized by changes in the number of individuals in each age/size class. There are two kinds of evidence for this: work such as that cited above, on the plasticity of individual behaviour in response to environmental change, and the present results at the group level, showing a complex moment-to-moment regulation of numbers doing each task in response to environmental change. Whatever types of individuals are present, what these individuals actually do is contingent on the current state of the colony's environment. This study raises a new kind of question about colony ontogeny: how do the group-level dynamics relating behaviour and environment change as a colony matures?

At the ecological level, ontogenetic changes in the flexibility of the daily round may be very important. The ways that colonies respond to my artificial perturbations should be analogous to the ways they meet changes occurring naturally in the food supply and obstructions on the foraging trails; debris blown or washed onto the nest mound, and other changes in nest structure brought about by weather and animals; alterations in the patterns of encounter with other ants, brought about by demographic shifts in community structure; and the intrusion onto the mound of various animals, harmless or predatory. In communities in which food is a limiting resource and the mortality of young colonies is high, the way a colony responds to environmental events may have important consequences for its survival. Even in very young colonies, perturbations reveal complex interactions between numbers engaged in patrolling, foraging and nest maintenance. The results further suggest that older colonies are more consistent and that as circumstances get worse, they decrease foraging less. By contrast, it appears that younger colonies will sometimes shift into various other activities, like patrolling or nest maintenance, as conditions worsen.

The ecological consequences of ontogenetic changes in daily round flexibility have yet to be investigated. The present work, and other observations, reveal both ontogenetic and interspecific variation in the ways that harvester ant colonies interact with their environments. Such variation may be crucial in the evolution of desert communities.

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