Behavioral Flexibility and the Foraging Ecology of Seed-Eating Ants

Deborah M. Gordon

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BEHAVIORAL FLEXIBILITY AND THE FORAGING ECOLOGY OF SEED-EATING ANTS

Deborah M. Gordon*

Department of Zoology, University of Oxford, and Centre for Population Biology,
Imperial College at Silwood Park, UK

Abstract.—Seed-eating ants are part of a guild of granivorous desert species that compete for food. This study examines the factors that influence the intensity, location, or temporal pattern of foraging in the red harvester ant, *Pogonomyrmex barbatus*. I consider behavioral flexibility on three time scales: year to year, day to day, and hour to hour. On a yearly time scale, there does not appear to be any simple relation between high intensities of foraging and survival rate. Colony-specific differences in foraging activity persist from one year to the next, but survivorship is not higher in colonies more likely to forage. Distributions of nests change from one year to the next and are usually underdispersed or clumped. Colonies live for 15–20 yr. Colony behavior is more stable, and more likely to avoid intraspecific conflict, in older colonies (>5 yr old) than in younger ones (2 yr old). Mortality rates of 2-yr-old colonies are similar to those of older ones. Other results suggest that a colony's competitive status is determined by its behavioral flexibility in changing conditions, on daily and hourly time scales. Each day that a colony forages, it chooses a few foraging routes out of a larger set of available ones. This decision is made early each day by the patrollers, a distinct group of workers, before the foragers emerge from the nest. The choice of foraging trails is influenced by interactions with neighboring colonies. The extent to which neighboring colonies forage on trails that intersect, and engage in long-term conflict, depends on colony age and food availability. When there is a food incentive, pairs of neighboring younger colonies are more likely than older pairs to continue using foraging trails that overlap. On an hourly time scale, the intensity of foraging depends on the rate of food intake and on the activities of workers, such as patrollers, engaged in other tasks besides foraging.

Behavior is the manifestation of an animal's relation with its environment. Environments change, causing behavioral patterns to change. This process is behavioral flexibility. The theme of changing conditions, and the capacity to respond to them, recurs throughout evolutionary biology. Morphology, development and life histories can be plastic, able to change when environments do (Bradshaw 1965; Caswell 1983). A combination of ecological variables may affect the evolution of flexibility, including the time scales of environmental change and the organism's response to it, and the advantages of adapting to a range of possible conditions (Levins 1968). Recent theoretical work shows that changing environments, and associated changes in the benefits of a phenotype, can have strong ecological effects. For example, patterns of environmental heterogeneity deter-

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* Present address: Department of Biological Sciences, Stanford University, Stanford, California 94305

mine the population dynamics of coexisting species, because as conditions change, both the population numbers and the benefits of each species' competitive phenotype change as well (Chesson 1986).

It is becoming increasingly clear that flexibility is an important aspect of the behavioral phenotype of many animals (Caro and Bateson 1986). This raises questions about the evolution and ecological role of behavioral flexibility. An example is Brown's (1989) theoretical work, which shows that temporal variation in foraging efficiency can affect the outcome of competition between two species. But empirical work on behavioral flexibility has not yet caught up to theoretical work on the evolutionary ecology of changing environments, or to empirical work on the plasticity of phenotypic characters other than behavioral ones. We know little about the relation between flexibility, survival, and reproductive success, or about the ways that the development of social behavior constrains the evolution of flexibility. Under what conditions does behavioral flexibility evolve? To answer this, we need to know how much flexibility exists, how it works, and when it matters.

This study addresses two questions about behavioral flexibility in colonies of the red harvester ant, *Pogonomyrmex barbatus*. First, when and why does a colony's behavior change? A complete answer to this question would spell out the dynamics linking the set of possible environmental conditions with the range of possible behavior. Such rules operate on several different time scales and on different levels of organization. An individual ant's behavior changes from one minute to the next, as chemical and social stimuli change. An ant colony's behavior changes from one day to the next, as weather, food availability, and its neighbor's behavior change. One goal of this study is to bring together investigations of flexibility from several different perspectives: short-term adjustment to environmental change by the internal organization of a colony, longer-term relations among neighboring colonies, and year-to-year, life-history changes in a colony's behavior.

A second question about flexibility in harvester ants is, What are its ecological consequences? Ecological studies of desert ant communities show that the distribution and abundances of seed-harvesting ants depend on interactions of many seed-eating species, including ants, birds, and rodents (Brown and Davidson 1977). Diffuse competition for food affects the foraging ecology of some species (Davidson 1985). Among harvester ant species of the genus *Pogonomyrmex*, both intra- and interspecific interactions affect colony distribution (Whitford et al. 1976) and spatial patterns of foraging (Hölldobler 1976*a;* Harrison and Gentry 1981). The behavioral mechanisms that maintain the ecological structure of desert communities are not yet understood. How does competition for food affect, and mediate, day-to-day interactions of colonies? How does each colony modulate its foraging behavior to take advantage of changes in food availability?

Because food is so crucial to the ecology of harvester ants, I will concentrate here on foraging behavior. There is some confusion in the literature on social insects about the term "foraging," which is sometimes used to refer to any behavior outside the nest. Here, by "foraging," I mean behavior concerned exclusively with the retrieval of food. Harvester ant foragers are easily distinguished from

exterior workers engaged in other tasks. In *P. barbatus,* foragers travel away from the nest on a common foraging trail, which may extend 10–40 m from the nest. At the end of the trail, they disperse, collect seeds or insect parts, and, traveling along the same trail, bring them directly back to the nest.

What causes *P. barbatus* colonies to change the intensity and spatiotemporal patterns of foraging? On the year-to-year time scale, I examine changes in the spatial distribution of nests, because the foraging behavior of a colony depends in part on its proximity to other harvester ant colonies. I consider some of the factors that affect the spatial distribution of nests: colony longevity and the relation between colony survival rates and foraging activity. On the day-to-day time scale, I explore the extent to which colonies change the location of foraging trails and how interactions among foragers and other worker groups, within a colony, lead to a decision about where that colony will forage each day. I then consider how foraging decisions are influenced by interactions between pairs of neighboring colonies, depending on colony age and food availability. On the hour-to-hour time scale, I look at how the rate of food intake, and interactions between foragers and other worker groups, affects the intensity of foraging.

The next section is divided into three parts, discussing, in turn, factors affecting foraging behavior on the yearly, daily, and hourly time scales. Within each part, I describe experiments or observations relevant to that time scale. Methods and results are presented for each experiment separately. In the final discussion section, I review previous work on behavioral flexibility in seed-eating ants and draw some general conclusions.

YEARLY TIME SCALE

A colony's behavioral flexibility is its short-term response to a changing environment. Some features of its environment change on a longer time scale. For example, a colony's foraging behavior is affected by the proximity of other nests. Mortality rates determine how quickly a colony's neighbors change. In a long-lived species, interactions between neighbors might emphasize the preservation of established foraging routes; in a short-lived one, immediate gain could be more important. The first two subsections of this part examine not behavioral flexibility, but two aspects of its ecological context: mortality schedules and patterns of nest distribution. In the third subsection, I consider the relation of foraging activity and survival rate.

Colony Longevity

Harvester ant colonies reproduce in an annual mating flight. Winged reproductives from an area of 120,000 m² (Hölldobler 1976*b*) converge at a single mating site. After mating, males die, and newly mated queens disperse randomly. Each surviving queen digs a new nest. The first workers emerge after 6 wk. Studies of other species in the genus suggest that colonies can live for 15 or 20 yr (see, e.g., Porter and Jorgensen 1988, for *Pogonomyrmex owyheei*), as long as the queen remains alive and continues to lay eggs (all fertilized by stored sperm from the original mating), producing the colony's workers and the reproductives that will

TABLE 1

COLONY LONGEVITY

Census Period	No. of Colonies Surviving through Period (Total No. in Age Group)	K_d	Mean Survival (yr)
1985–1988 old	18 (25)	.22	9.5
1985–1988 young	25 (39)	.15	21.6
1986–1988 old	28 (47)	.26	12.9
1986–1988 young	18 (25)	.17	17.3
1986–1988 intermediate	7 (11)	.22	10.9

NOTE.—The table shows mortality data for two census periods, classified by the ages of colonies in the first year of the period. Mean survival is the number of years a colony would be expected to survive at the indicated mortality rate. Colonies of intermediate age are 3–4 yr old.

disperse in the yearly mating flights. If a colony's queen dies, it appears that *Pogonomyrmex barbatus* colonies do not adopt new queens from the same or other colonies (MacKay 1981). In a queenless colony, workers continue to forage and maintain the colony and to produce trophic and male eggs (D. M. Gordon, personal observation, for *Pogonomyrmex badius*). Once a worker joins the exterior work force, it may survive for another 6 wk (Gordon and Hölldobler 1988). The colony disappears when all existing workers have died.

I visited the same study site near Rodeo, New Mexico, every summer from 1981 to 1989, with the exception of 1983. Detailed maps of all *P. barbatus* colonies in an area of about 8 ha were made each year, beginning in 1985. Ages of colonies can be estimated (as in Gordon 1987) from maps made in previous years and measurements of nest size, since, during the first 5 yr of a colony's life, the cleared nest mound area gets larger from one year to the next. Like other *Pogonomyrmex* species (Porter and Jorgensen 1988), *P. barbatus* colonies sometimes move into abandoned nests. It seems that most moves take place after the summer rains, at times when I have been at the study site and able to observe which colonies moved. Nest relocation can take many days, and during this time a colony may appear to occupy more than one nest mound. However, observations of marked individuals (Gordon 1989a) indicate that, unless they are moving, colonies are not polydomous. To my knowledge, a colony never evicts another active one and takes over its nest. For the census and mapping data reported here and below, only colonies seen to be active in successive years were considered to be the same colony in both years' maps. If a colony appeared to be barely active one year and thriving the next, it was possible that a new colony had entered the new nest. In these cases, or whenever colony identity was questionable, data for those colonies were not included here.

Beginning in 1985, I was able to discriminate between "young" colonies, less than 2 yr old, and "older" colonies, at least 5 yr old. In the summers of 1986, 1987, and 1988, I checked all surviving colonies. Mortality rate (per year) of colonies (K_d) and colony longevity were estimated according to the methods of Chew (1987) (table 1).

TABLE 2

DISTRIBUTION OF NESTS

Year	No. of Colonies	Density (no./ha)	Mean Nearest-Neighbor Distance (m)	Expected Nearest-Neighbor Distance (m)	P
1985	74	9.8	12.9	15.2	.05
1986	97	11.8	11.5	15.2	.01
1987	130	14.9	10.9	15.2	.01
1988	178	21.9	10.8	10.9	NS

NOTE.—Expected nearest-neighbor distance is the expected value of the mean nearest-neighbor distance if distributions are random. P is the significance level of the test for nonrandom distributions (Clark and Evans 1954).

The average mortality rate per year is 0.20. Mortality among founding queens is much higher (Hölldobler 1976a). The present results do not show any tendency toward higher juvenile mortality but suggest that, once a colony is successfully founded and survives to be 2 yr old, its chances of further survival are similar to those of older colonies. It appears that in *P. barbatus,* as in other *Pogonomyrmex* species, colonies can survive for 15 or 20 yr.

Previous results, described in Discussion below, show that a colony's behavior changes as it grows older. Juvenile mortality is no higher than that of older colonies. This implies that the behavior of younger colonies does not have an adverse effect on colony survival, relative to the behavior of older ones.

Distribution of Nests

The overall pattern of nest distribution may affect foraging intensity. If so, changes in this pattern would cause foraging behavior to change. For example, if a widely spaced distribution of nests were the norm, a colony could be constrained by especially crowded conditions. Here I examine long-term patterns of nest distribution, and whether such patterns change from year to year.

In the ecological literature on harvester ants, there seems to be general agreement that *P. barbatus* colonies are overdispersed, as a result of intraspecific and interspecific competition. However, it is not clear on what data this conclusion is based; the studies usually cited (e.g., by Levings and Traniello 1981) do not support it. For example, Whitford et al. (1976) reported that, intraspecifically, the distribution of *P. barbatus* colonies is random; Hölldobler (1976a) reported nearest-neighbor distances but not dispersion patterns; and Davidson (1977) did not mention intraspecific colony distribution in *P. barbatus*. Recent authors have also pointed out that the relation between overdispersion and competition does not necessarily hold (Ryti and Case 1986).

In three years of measurements of the locations of active colonies, I found no evidence for overdispersion. In 1985, 1986, and 1987, colonies were significantly underdispersed or clumped, according to the test in Clark and Evans (1954) (table 2). Sinclair (1985) suggests that Clark and Evans's test may not be valid for samples less than 100, so the result for 1985 may be discounted. In 1988, the distribution

of colonies was random. A comparison of distributions in 1986, 1987, and 1988 showed that they are significantly different (F-test [Clark and Evans 1954], F = 14.6, df = 2,402, P < .001), apparently because of the random rather than clumped distribution in 1988. Thus, distributions are not stable from year to year, and measurements of dispersion made in only one year cannot be taken as definitive for the species.

Previous authors suggested that colony location depends on the avoidance of crowding (e.g., Hölldobler 1976a; De Vita 1979; Harrison and Gentry 1981). The patterns reported here suggest that this is at best a partial explanation. A colony's location seems to depend as well on finding a suitable site. Suitable sites may be clustered, though there were no physical barriers apparent to me, such as vegetation, to account for the clumping of nests. In 1985, colonies may have settled only at the most desirable sites. These became more crowded each year as density increased. The shift from a clumped spacing in 1985–1987 to a random distribution in 1988 could be caused by increased crowding. That is, more colonies could have appeared between the original clumps of colonies, leading to a somewhat more homogeneous, random distribution. Average nearest-neighbor distances at this site, ranging from 10.8 to 12.9 m (table 2), are smaller than those reported by previous authors. For example, Hölldobler (1976a) reports an average distance of 18.1 ± 5.3 m (n = 35). But until 1988, the densities here, from 9.8 to 21.9 colonies per ha, were lower than those previously reported. For example, Whitford et al. (1976) report a density of 22 colonies per ha. The combination of low nearest-neighbor distances and low densities found here may be due to clumping into suitable sites.

Year-to-year changes in the distribution of nests may reflect differential rates of colony foundation and mortality, and changes in the factors affecting nest relocation (Gordon 1990). The spatial distribution of nest sites gives only a partial measure of the intensity of interaction among neighboring colonies. Experiments described below show that such interactions also depend on a colony's day-to-day decisions about where to forage.

Colony-specific Variation in Foraging Activity, and Colony Survival Rate

Variation among colonies in foraging behavior may reflect colony-specific differences, flexibility, or both. Here I consider two ways in which colony-specific differences are relevant to the understanding of flexibility. First, the two should not be confounded: the range of intercolony variation may not reflect the extent to which each colony can change its behavior. Second, colony-specific differences in the level of foraging activity may affect patterns of colony survival. Patterns of survival affect nest-site distributions, which in turn determine distances between neighboring nests and thus affect foraging behavior.

Colonies differ from each other in the extent of their foraging activity. For 41 d in the summer of 1986, 77 colonies were observed, and for 37 d in the summer of 1987, 132 colonies were observed. Each day, during the daily peak of foraging (at about 8:30 A.M.), each of these colonies was classified as "foraging actively" if there was a strong foraging trail, as "barely foraging" if only a few ants were observed outside the nest and there was no foraging trail, or as "not

active" if no ants at all were observed outside the nest in the course of several minutes. On some days, most colonies foraged actively, and on others, few did. For example, in 1986, the percentage of colonies foraging actively ranged across days from 30% to 94%.

Within each year, there were colony-specific differences in the number of days a colony foraged actively. Some colonies usually foraged; some rarely did. For 77 colonies, including both young and old ones, I compared the numbers of days the colony foraged actively in 1986 and 1987. The number of days a colony foraged actively in 1986 (out of 41) was significantly correlated with the number of days the same colony foraged actively in 1987 (out of 37; Spearman rank correlation, $n = 77$, $\rho = 0.38$, $Z = 33.3$, $P < .001$). Thus, there is persistent, colony-specific variation in the extent to which a colony forages.

I then examined the relation between a colony's tendency to forage actively and its survival from one year to the next. If this relation were strong, many of the colonies that died in a given year would have foraged actively for only a small number of days in the preceding year. For each colony, I derived the proportion of days on which it foraged actively. I compared the frequency distribution of this proportion of colonies alive the next year with the same distribution for colonies that were dead or never foraged actively the next year. This comparison was made for 1986–1987 and for 1987–1988.

In both the 1986–1987 and 1987–1988 comparisons, there were no significant differences between the proportion of days foraging actively in colonies that survived to the next year and the proportion in colonies that did not (two-tailed Mann-Whitney U-test: for 1986 and 1987, NS, $P = .22$; for 1987 and 1988, NS, $P = .31$). In 1987, the percentage of days a colony foraged actively ranged from 27% to 95%; of these colonies that were dead in 1988, the percentage of days they had foraged actively in 1987 ranged from 37% to 70%. Similarly, the range for the percentage of days active in 1986 was 22% to 100%; for the portion of these colonies that were dead in 1987, the range was 24% to 98%. This implies that the number of days a colony forages one year does not determine whether it survives to the next year.

Although there is considerable day-to-day variation in foraging intensity (described below), these results show that inactivity on the day-to-day time scale does not have immediate, drastic consequences for survival on the yearly time scale. Colonies vary in their tendency to forage actively. This tendency may be a summed response to all the factors involved in the dynamics of foraging intensity. A phenotype that results in relatively few days of foraging does not appear to threaten the colony's survival from one year to the next. Colony variation in reproductive success will be examined in future work.

DAILY TIME SCALE

Day-to-Day Variation in Foraging Intensity

Day-to-day changes in environmental conditions cause foraging behavior to change. On a given day, colonies vary in the intensity of foraging (see the subsec-
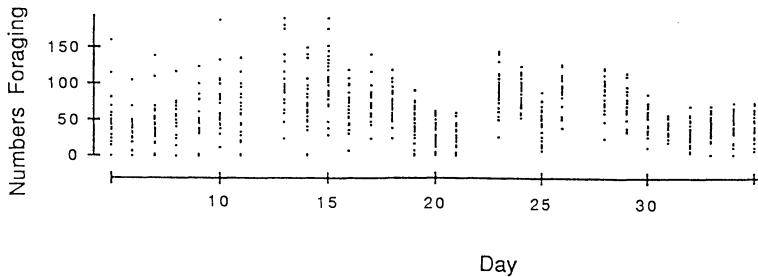
FIG. 1.—Day-to-day variation in the intensity of foraging. Each point represents the number of ants foraging within 1.3 m of the nest entrance at 8:00 A.M. in one colony.

tion Colony-specific Variation, above). But the numbers foraging also vary from one day to the next. One way to see this is to examine the intensity of foraging in a group of colonies across time. Figure 1 shows the numbers foraging at the peak of foraging activity, between 8:00 and 9:00 A.M., within 1.3 m of the nest entrance, in 37 colonies on about 30 d (data from undisturbed colonies in experiments O1–O4 in Gordon 1987). On some days, numbers foraging are high in most colonies; on others, most colonies do little foraging.

Foraging intensity seems to be strongly affected by weather. On the day after it has rained, foraging is often high; after several days of high temperatures and no rain, foraging activity often decreases (D. M. Gordon, personal observation). In other *Pogonomyrmex* species, foraging activity increases when the soil is wet (Whitford and Ettershank 1975). In addition, there are seasonal patterns of reproduction, and when large amounts of brood are present, colonies need more food. MacKay (1981) found seasonal fluctuations in amounts of stored seeds in large samples of *Pogonomyrmex* colonies. Day-to-day variation in foraging intensity may be due to weather conditions, changes in colony hunger level, and other unknown factors. Some possible explanations for the variation shown in figure 1 are given below.

Colony Organization and Decisions about Trail Location

Each day a colony chooses from a set of trails.—Is a *Pogonomyrmex barbatus* colony flexible in the location of the foraging trails it uses each day? Hölldobler (1974, 1976a) reported that a *P. barbatus* colony forages on a stable system of permanent foraging trails. This implies that trail location is not flexible. To examine whether the location of foraging changes from one day to the next, my assistants and I mapped the trails used by 30 colonies on 8 d in 1988, with an interval of 2–4 d between maps. The colonies mapped consisted of 14 pairs or triads (groups of three) of adjacent colonies. The ages of colonies mapped ranged from 3 to at least 7 yr old. Each pair or triad contained colonies of a similar age, except for one group of one 2-yr-old and two 5-yr-old colonies. Maps were made with a string grid with four 23.1-m lengths arranged as a star in N-S, E-W, NW-SE, and NE-SW directions. The string was marked at 1.5-m intervals on the compass directions. String grids were placed at the same site for each mapping session,
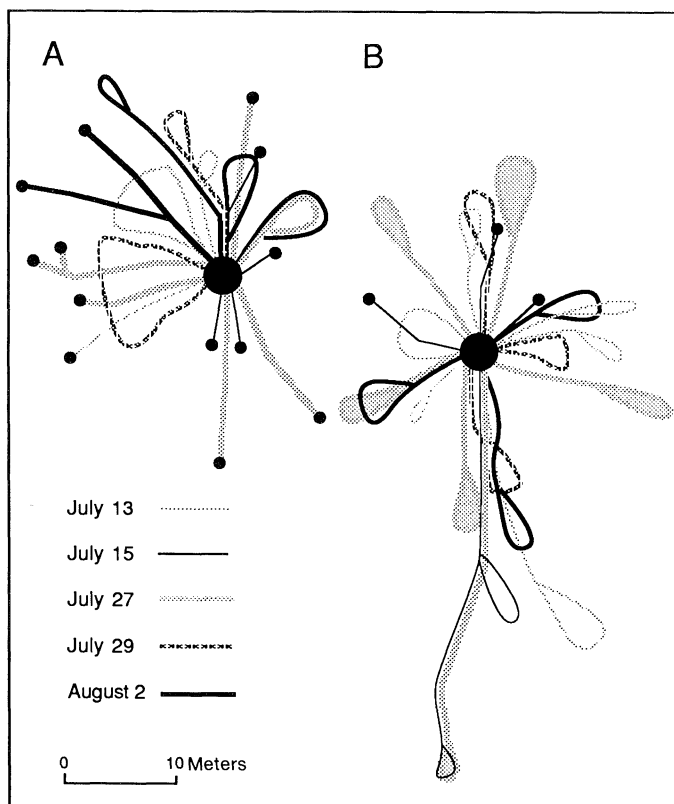
FIG. 2.—Foraging trails of two colonies. Each day's trails are represented by a particular design. Large filled circles represent the nest mounds. If the trail ended in one shrub, this is shown with a small filled circle. Otherwise the outline of the area in which foragers fanned out is shown. Mapping methods are described in the text.

on stakes that remained in place throughout the study. The maps were accurate to within 0.5 m. Maps were made during the period in which colonies chose and extended their trails for the season; maps were begun during the first burst of foraging activity after summer rains began, and they were continued for 5 wk throughout the most active foraging season of the year.

Each map showed the location of all nest entrances and trails. A trail was drawn when five or more ants were seen passing a designated imaginary line perpendicular to the trail within 20 s. To ensure that trails persistent throughout a day were mapped, two counts of foragers were made each day on each mapped trail. The trail was shown to fan out when it became wider than 30 cm. If a trail went directly to a bush, this was noted. If not, the trail was considered to have ended at a certain point when no ants were visible within a 1-m radius of the point for 10 s. All observations of fighting were recorded.

Colonies do not use the same foraging trails every day (fig. 2). Each of the 30 colonies mapped had a set of trails, and only a few of this set were used on any
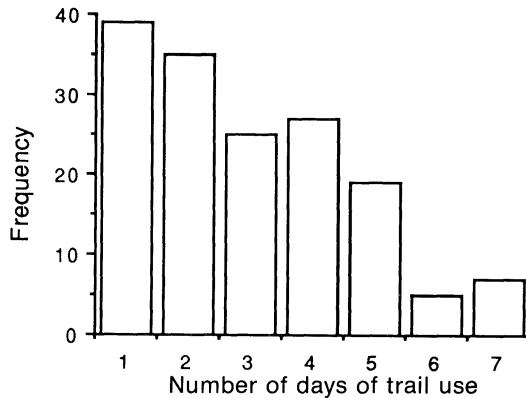
FIG. 3.—Frequency of trail use

given day. Most trails were used only once in 8 d of mapping. Figure 3 shows the frequency of trail use in 30 colonies in 7 d of mapping; a total of 169 trail-days are included. Few trails were used on all 7 days. A *P. barbatus* colony does not use the same foraging trails each day.

Exploration of trails by patrollers.—How does a colony decide which trail to use each day? Food sources can be divided into two kinds: new ones, and familiar ones, such as the plants from which seeds have been taken on the preceding days. A group of workers distinct from the foragers—I call them patrollers—finds new food sources and recruits foragers (Gordon 1983). Patrollers are active early in the morning, and patrolling activity has ceased by the time foragers become active. If a new food source is offered later in the day, after patrolling activity has ceased, foragers ignore it. In undisturbed colonies patrollers do not engage in other activities such as foraging (Gordon 1989a). But if an abundant new food source becomes available early in the morning, patrollers will recruit others to it and then join the foraging trail themselves, helping to retrieve the seeds. Here I examine the role of patrollers in day-to-day decisions about trail location in undisturbed colonies.

Patrolling is performed each day according to characteristic spatial and temporal patterns. Each morning the patrollers first emerge from the nest and walk around slowly near the nest entrance, waving their antennae and standing in a raised position with straightened front legs if there is a disturbance. They appear to be guarding the nest entrance. As other workers (mostly nest maintenance workers clearing sand from inside the nest) begin to emerge, the patrollers begin to walk more quickly, in a zigzag path, around the surface of the mound, often stopping to inspect other ants with their antennae. Later, some patrollers move out onto the foraging trails. Trail patrollers' behavior appears different from that of foragers; their movements are more hesitant, they perform antennal contacts with other ants more frequently, and they appear on the trails earlier than foragers.

Observations were made to determine, first, whether the early nest entrance patrollers, nest mound patrollers, and trail patrollers were each composed of

TABLE 3

Results of Experiments with Marked Patrollers

	Midden Work	Nest Entrance Patrolling	Nest Mound Patrolling	Trail Patrolling	Foraging	Nest Maintenance
Mound patrollers marked:						
Colony 55:						
Unmarked	167	95	184	725	542	540
Marked	8	3	31	44	5	0
Colony 146:						
Unmarked	64	110	410	616	344	582
Marked	11	8	87	68	1	0
Trail patrollers marked:						
Colony 50:						
Unmarked	46	87	172	466	143	306
Marked	1	37	99	131	4	0
Colony 68:						
Unmarked	79	84	158	683	176	633
Marked	3	25	44	70	1	2

Note.—Entries are the total numbers counted in 1 d within 1.3 m of the nest entrance, engaged in the indicated activities, in a series of counts at 10-min intervals.

distinct groups of individuals. In each of two colonies, 52 ants were collected when patrolling on the nest mound, marked with colored paint, and returned to the nest (all marking and observation procedures were as in Gordon 1989a). On the next day, counts were made at 10-min intervals of the numbers of marked and unmarked ants engaged in each of five exterior activies: nest entrance patrolling, nest mound patrolling, trail patrolling, foraging, and nest maintenance. Intervals of 10 min were chosen because most individuals' trips outside the nest are of shorter duration, which means that an ant could change tasks in that interval; thus each count can be considered independent of the others. Second, to determine whether trail patrollers also act as foragers, trail patrollers were marked. In each of two colonies, 76 patrollers were collected from foraging trails, marked, and released. Counts were made the next day as above. The results are shown in table 3.

Ants marked as patrollers were later observed to patrol. In all four colonies, the distribution of marked and unmarked workers among the five activities was nonrandom (G-test for heterogeneity, $G = 25.4–114.8$, for the 4 colonies, df = 5, $P < .01$). In all four colonies, marked mound or trail patrollers tended to specialize in mound or trail patrolling, rather than in nest entrance patrolling (using only total counts of marked ants in three categories of patrolling, $\chi^2 = 10.4–51.3$, df = 2, $P < .05$).

In one colony, counts were made at 5-min intervals of the numbers of ants engaged in nest entrance, mound, and trail patrolling. All ants engaged in these three activities, defined as in the second paragraph of this section, were counted within 1.3 m of the nest entrance, or on the first 2 m of all foraging trails beginning from the outer edge of the mound. The day's patrolling activity ends during the
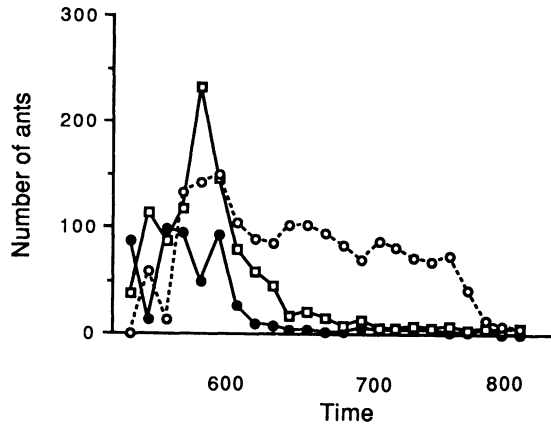
FIG. 4.—Temporal pattern of nest entrance, nest mound, and trail patrolling. Counts of numbers engaged in three types of patrolling are shown for one colony. *Filled circles*, nest entrance patrollers; *open squares*, nest mound patrollers; *open circles* and *dotted line*, trail patrollers.

onset of foraging (Gordon 1983), so counts of patrollers were ended when the first 20 foragers had been observed returning to the nest entrance with food. Figure 4 shows the resulting temporal pattern of patrolling in this colony.

Trail patrollers and foragers tend to be two distinct groups of individuals. Mound and trail patrollers do not appear to be distinct groups of individuals. It appears that within each day, patrollers move sequentially from nest, to mound, to trail patrolling. Each morning, patrollers go out on the trails before the foragers do.

Patrollers choose the day's trails.—Flexibility in the location of foraging trails seems to be based on interactions of patrollers and foragers. Patrollers explore the trails before the foragers do, and recruitment to new food sources takes place only when patrollers are active. As well as searching for and recruiting workers to new food sources, patrollers may influence a colony's decision about whether to use trails toward familiar food sources. A colony does not use all of its foraging trails every day. Does it tend to use the previous day's trails? Here I examine how the location of patrolling and foraging on one day is related to the location of foraging the day before. Observations were made to determine whether a colony tends to forage only on the trails explored that morning by its patrollers, and whether the patrollers tend to explore the foraging trails used on the previous day.

The directions taken by patrollers were mapped with the string grids described above. Observations began when patrollers were first observed emerging from the nest and continued for 20–50 min, until foraging was well under way. Observations ended when 20 foragers had been seen coming back to the nest on a trail with food. The observer circled the nest entrance in concentric circles 1.5 m apart, spreading to include all patrollers noticed, and repeated this process at 10-min intervals. During this time, the locations of all patrollers observed were

recorded on the map. Patrollers were identified as in Gordon (1987, 1989a); patroller behavior is described in detail in the preceding section. Later in the day, all foraging trails were mapped. Nine maps of patroller location were made on different days for seven colonies. Numbers of patrollers whose locations were recorded ranged from 30 to 153 per colony-day. In all nine cases, the colonies' foraging trails had also been mapped on the preceding day.

Several hypotheses were considered. (1) There is no relation between the direction from the nest taken by the patrollers and the colony's subsequent choice of foraging trails used that day. (2) Patrollers explore only the trails used on the preceding day. If the colony forages that day on any fallow trails, that is, trails not used on the preceding day, the decision to use these is made later in the day by the foragers. In this case, foragers would use either yesterday's trails, explored that morning by the patrollers, or other trails explored later on by foragers. Recruitment to fallow trails would then not be initiated by patrollers but would depend instead on some assessment by foragers of the food encountered. (3) Patrollers explore both some trails used the preceding day and some fallow trails. Later on in the day, the patrollers' choices persist; foragers use the trails explored by patrollers. This third hypothesis was confirmed.

The data were analyzed according to the method of Marriott (F.H.C. Marriot, unpublished manuscript). The problem was to detect an association between the distribution of the directions taken by the patrollers and the directions of the foraging trails (on the same day or the preceding day). The direction from the nest entrance taken by each patroller and the direction of each foraging trail were measured in degrees on an imaginary circle around the nest entrance. The patrollers' directions were in general not uniformly distributed on a circle, and distributions were multimodal. The question is whether the directions of foraging trails tend to favor the denser parts of the distribution of patrollers' directions.

The method involves estimating a probability density corresponding to the sample of patroller directions on the day of observation. For each day and colony, the density was smoothed with normal kernels (Silverman 1986) of a standard deviation, σ, of 5.6 degrees ($=0.1$ radians). Figure 5 shows the smoothed density of patroller directions for one day (day S) and colony. The null hypothesis is that the directions of foraging trails are random and unrelated to the distribution of patrollers' directions. This was tested first for trails of the same day and then for trails of the preceding day. Figure 5 shows the directions of foraging trails both on the same day (day S) and on the preceding day (day P). For smoothed density taken as $f(\theta)$, with a mean μ and standard deviation s, and $\log f(\theta_i)$ calculated for each i of the n foraging trails, $z = \Sigma [\log f(\theta_i) - \mu]/[s(n^{1/2})]$ has zero mean and unit variance on the null hypothesis and was tested as a standard normal deviate.

Foraging trails on a given day were significantly likely to follow the direction taken by the patrollers earlier that morning ($n = 37$ for all trails on the same day as all nine colony-days of observation, $P < .02$). This rules out the first hypothesis listed above, that the directions of foraging trails and of patrollers are unrelated. However, patrollers were also likely to take the direction of the preceding day's foraging trails ($n = 37$ for all trails as above on the day preceding the day of observation, $P < .02$). But often foragers used the same trails both on the day of
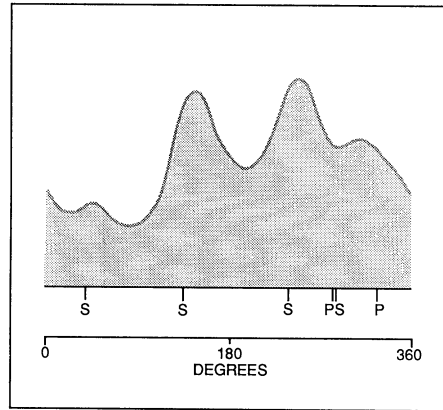
FIG. 5.—Directions taken by trail patrollers and by foragers. The horizontal axis represents, in degrees, the directions taken from the nest entrance by trail patrollers and the direction of foraging trails. The vertical axis represents the probability density of patroller directions on day S. The curve shows the estimated probability density function of the directions taken by 66 patrollers in one colony on one day (day S); the area under the curve is 1. Small vertical lines show the direction of foraging trails on the same day as observations of the patrollers (S) and on the day preceding observation (P).

observations of patrollers and on the preceding day. The analysis was repeated after eliminating those foraging trails used both on the same day and on the preceding day that fell within 10° of each other. This left two classes of foraging trails: those used by foragers on the preceding day but not on the day of observation, and those used by foragers on the day of observation but not on the preceding day. The patrollers were found on the latter. When patrollers explored directions that did not correspond to the foraging trails of the preceding day, these were the directions of foraging trails on the day of observation (n = 24, P ≪ .001). This rules out the second hypothesis listed above. Patrollers are not constrained to explore only the trails used by foragers on the preceding day. When patrollers do explore fallow trails, these trails are used later on in the day by foragers. Patrollers did not explore the first class of trails, those used by foragers on the preceding day but not used later by foragers on the day of observation (n = 14, P = .15, NS). Taken together, these results confirm the third hypothesis listed above. Patrollers explore a variety of trails each day, including both the trails of the day before and other, fallow trails. Later each day, foragers use the trails that were most intensively explored by patrollers.

On a given day, colonies use the trails explored that morning by the patrollers. The patrollers' day-to-day choices of foraging trails may depend on patrollers' using two kinds of information. First, patrollers may obtain, from foragers, information about the quality or abundance of food on various trails on the preceding day. This requires communication between distinct worker groups. The results of previous experiments make it apparent that such communication exists (Gordon 1989a). The mechanisms are not yet understood. A second source of information

may be that detected by patrollers themselves about the quality or abundance of food available on various trails during their early-morning exploration. Recruitment by patrollers to new food sources, observed in previous experiments, would be one aspect of this second category. Recruitment to abundant new food sources causes a dramatic response in which workers previously engaged in other tasks are recruited to forage (Gordon 1989a). But it appears that patrollers also signal regular foragers that a particular trail is worth using. This seems to be an everyday event, occurring even when the trail does not merit a special, strong recruitment effort drawing on other worker groups to join the forager force.

Trail fidelity of foragers.—One mechanism for flexibility in the location of a colony's foraging may be flexibility of individual foragers in which trails they use. Hölldobler (1976a) reported that, in *P. barbatus,* individual foragers tend to remain on particular trails. His experiments were made in conditions of stable food resources, but, as we have seen, different foraging trails are used on different days. In addition, the numbers of ants on trails change as food availability fluctuates. This means that ants must be added to and removed from particular trails. When this happens, do foragers move from one trail to another? An alternative might be that an individual forager always uses a particular trail if she forages, while new foragers are added to trails, when needed, from reserves inside the nest. To examine the relation between individual trail fidelity and colony decisions about changes in the allocation of workers to different trails, an experiment was conducted with marked individuals.

In each of three colonies, 200–250 foragers from one trail were marked and replaced according to the same methods described above for experiments with marked patrollers. On the second day, a second trail was created by putting out a seed bait. Seven counts were made at 20-min intervals of the numbers of foragers in the first 2 m of each trail, beginning at the outer edge of the nest mound. Counts were made of all trails, including the original trail, the new bait trail, and all remaining trails (zero to four remaining trails in the three colonies).

The results (table 4) show that, when a new food source becomes available, foragers change trails. In all colonies, there was strong recruitment of foragers to the seed bait. Marked foragers, following the general trend among all foragers, changed from their original trail to the new one. In two of the three colonies the proportions of marked ants were similar to the proportions of unmarked ants (χ^2 test, df = 1: colony 175, $\chi^2 = 2.05$, NS; colony 142, $\chi^2 = 6.1$, NS). There was also clear evidence for the existence of trail fidelity: marked foragers were observed on their original trail or on the new bait trail, but rarely on any of the remaining trails (see data for colonies 162 and 142, table 4). The proportions of marked ants on original, bait, and other trails were significantly different in both of these colonies (χ^2 test, df = 3: colony 162, $\chi^2 = 94.8$, $P < .01$; colony 142, $\chi^2 = 40.6$, $P < .01$).

Trail fidelity has been most clearly demonstrated in formicine ants (Rosengren and Fortelius 1986), usually under experimental conditions in which the location and abundance of food are stable. Although Fewell (1990) emphasized the existence of trail fidelity in *Pogonomyrmex occidentalis,* her results with food baits suggest that, in this species as well, foragers change trails in response to new

TABLE 4

FORAGERS CHANGE TRAILS IN RESPONSE TO SEED BAITS

	Original Trail	Bait Trail	Sum of Remaining Trails
Colony 175:			
Unmarked	202	286	No other trails
Marked	35	72	
Colony 162:			
Unmarked	279	729	780
Marked	44	44	1
Colony 142:			
Unmarked	125	439	282
Marked	34	67	7

NOTE.—Entries are total numbers of marked and unmarked foragers observed in 1 d on the original trail (on which foragers were marked on the preceding day), on the new trail to a seed bait, and on the sum of all remaining trails.

food sources. In *P. barbatus,* it is clear that individual trail fidelity exists, but it does not persist when there is a change in the allocation of workers among different foraging trails.

Interactions between Neighboring Colonies

The foraging behavior of one colony may be affected by that of its neighbors. In this section I examine how a colony's neighbors may inhibit or facilitate its foraging activities. On a day-to-day time scale, how do colonies interact with each other? The most thorough study to date, and the one most frequently cited, of intraspecific territorial behavior in harvester ants is that of Hölldobler (1974, 1976a), conducted across the road from the site discussed here. Hölldobler's study, and its interpretation in subsequent citation, portrays a population of harvester ants as consisting of colonies with established, permanent foraging trails. Foraging trails of neighboring colonies diverge, because a meeting between workers of neighboring conspecific colonies "invariably leads to fierce fighting" (Hölldobler 1974, p. 3274). Studies of other seed-eating species also report that trails of neighboring colonies never intersect (Ryti and Case 1986; Harkness and Isham 1988).

These conclusions raise several questions about territoriality in seed-eating ants. If trails never meet, how do colonies continue to be informed of one another's existence? As a young colony develops its trunk trails, how does it arrange its trails so as not to intersect those of its neighbors? Of all exterior workers, it is the foragers and patrollers that usually leave the nest mound to search for and retrieve food (Gordon 1984). Foragers distinguish ants of neighboring colonies from ants of more distant colonies (Gordon 1989b). This implies that workers from neighboring colonies interact frequently enough to learn to recognize colony-specific odors. The most frequent occasion for direct interaction between colonies may be when neighboring colonies explore foraging trails that meet.

Effect of colony age on interactions between neighboring colonies: observations.—The trails of neighboring colonies do intersect, but this does not always
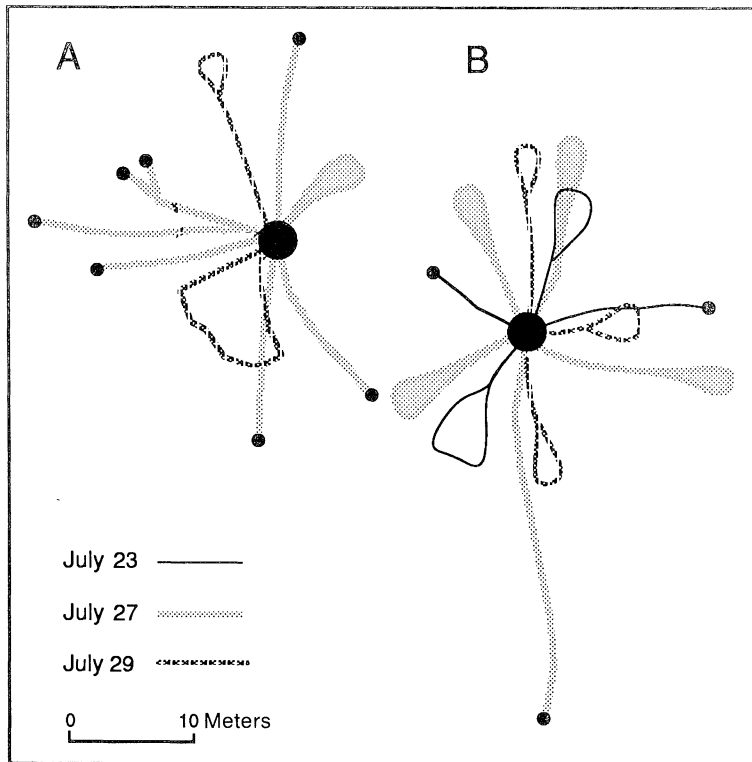
FIG. 6.—Intersection of trails of two older colonies. Each day's trails are represented by a particular design. Large filled circles represent the nest mounds. Trails meet on July 27. On July 29, trails are used that avoid the region of intersection.

lead to fighting. Figure 6 shows the trails for 3 d for the same two colonies shown in figure 2. These two colonies have been neighbors since at least 1981, at similar distances from each other. The sequence shown in figure 6 is typical of trail intersections in undisturbed pairs of older colonies. On July 23, colony A was not active; on July 27 trails from the two colonies met, and no fighting was observed; on July 29 the two colonies foraged away from each other. That is, foragers used trails that avoided the site of intersection. It seems that such a sequence of events is fairly common. In the course of 8 d of mapping (in 1988), a sequence like this was observed in four of seven pairs of undisturbed colonies. No fighting was observed in any of these undisturbed colonies.

In pairs of younger colonies, however, the intersection of trails sometimes continued for many days, and fighting was often observed. For example, figure 7 shows maps of the trails of 3 colonies over a period of several weeks in 1988. Colony 43 was 5 yr old; colonies 162 and 169 were each 3 yr old. Figure 7 shows that from July 13 to July 27, trails avoided each other. On July 30, the trails of colonies 162 and 169 began to meet. The use of intersecting foraging trails, and
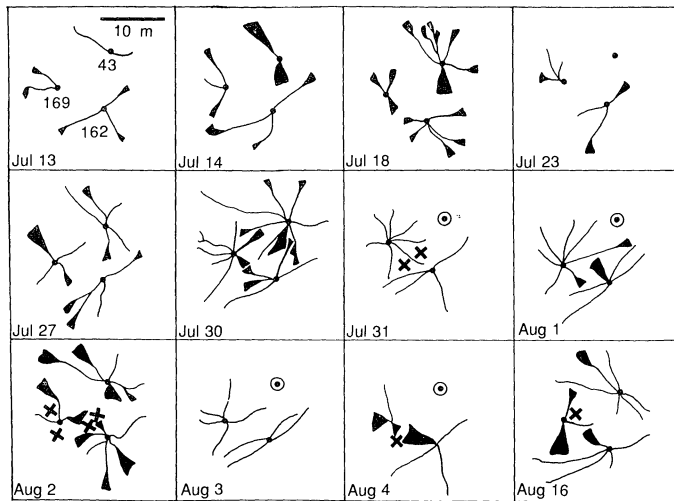
Fig. 7.—Intersection of trails of younger colonies. A sequence of maps of the trails of three younger colonies over several weeks is shown. Numbers identifying the three colonies are shown in the first drawing (July 13). Small filled circles represent nest mounds. A circle with no trails indicates that the colony was not active that day. A circle surrounded by a larger one indicates that no maps were made of that colony on that day. Trails begin to intersect on July 30, and continue to do so on subsequent days. ✖ indicates fighting between pairs of ants.

fighting between pairs of ants, continued for the next 4–6 d. Ten days later, and 17 d after the trails first intersected, on August 16, trails continued to meet and fighting was still observed. These younger colonies seem to have stablized in a condition of territorial conflict.

The observations above show that, at least in younger colonies, fighting is not always sufficient to cause colonies to abandon foraging trails that intersect with those of a neighbor. Observations do not show whether the use of trails that avoid those of a neighbor might not have occurred anyway, independently of interactions with neighbors; experiments are required for this. The following experiments examine how the magnitude of a food incentive and the age of a colony affect a colony's tendency to use trails that intersect with those of a neighbor. Here and below, in considering effects of colony age, it is important to note that colony age is correlated with colony size; colonies contain more workers as they grow older. Effects of colony age may be effects of colony size.

The effect of a food incentive on interactions between neighboring colonies.— On what time scale do colonies respond to changes in the foraging behavior of their neighbors? Other studies have shown that placing a line of seeds between two colonies causes them to fight (Hölldobler 1976a; Bailey and Polis 1987). Here I placed seeds close to the nest of one colony to test whether increased food availability for one colony would affect the foraging behavior of a close neighbor.

Experiments were conducted in 1988 with the 30 colonies in which trails were

mapped as described above. There were 14 groups or pairs of colonies, each of which was out of reach of the other 13. These were divided into two treatment groups, each containing six pairs and a seventh group of three adjacent colonies (all called "pairs" in the following). Seven pairs were left undisturbed and unfed, as controls. In each of the other seven experimental pairs, one colony was designated weaker and one stronger, according to numbers foraging. A line about 1 m long (about 15 g) of mixed birdseed, mostly millet, was placed from an existing trail of the weaker colony toward, but only to within 2 m of, an existing trail of the stronger colony. Seeds were put down for 10 d each morning when the patrollers were first active, before foraging began, to encourage recruitment to retrieve the seeds (Gordon 1983). In all colonies three counts per day were made, at 2-h intervals, of the numbers of ants engaged in foraging, on all trails, within 1.3 m of the nest entrance (techniques as in Gordon 1986). These observations were made for 3 d before the experiment began, and on days 1, 2, 3 and days 7, 8, 9 of seed bait trails. In all experimental colonies, maps of the directions of foraging trails, and counts of numbers of ants fighting, were made twice daily on all 10 d of seed baits. The maps were also made for 7 d after seeds were no longer put out, at two 1-h intervals during the time of day that foragers were most active.

In every experimental pair, the stronger colony departed from its usual trail to collect the weaker colony's seeds. The weaker colonies branched off from their usual foraging trails to collect the seeds as well. Most of the 15 experimental colonies foraged toward the seeds (fig. 8). This continued even after seeds were no longer offered.

Although seeds were placed near the weaker colony, this spatial advantage did not usually alter the imbalance between pairs, in numbers foraging, that existed before the experiment began. The weaker colony in each pair tended to forage less than the stronger one throughout the 10 d of seed trails. The counts of numbers foraging were used to calculate the difference, at each observation, between the numbers foraging in the weaker and stronger member of each pair of experimental colonies. In the three-colony group, data for the two stronger colonies were averaged to calculate this difference. Colonies were observed three times daily, so there were three such differences per day per colony pair. In the first observation each day, made between 5:30 and 7:30 A.M., counts of foraging were almost always zero in all colonies; these data were not analyzed further. Differences for the second and third daily observations were each used in a separate ANOVA examining the effect of observation period (3 d before the experiment, days 1–3, days 7–9), colony pairs (7), days within observation period (3), and the colony pairs by observation period interaction.

At the peak of foraging, between 7:30 and 9:30 A.M., there was no significant effect of observation period (sum of squares = 751.81, F = 0.89, df = 2,36) on differences between colony pairs. That is, differences between members of each pair in numbers foraging did not change after the experiment began, compared with such differences in the first observation period before the experiment began. There were, however, significant effects of colony pairs (sum of squares = 23,086.45, F = 9.08, df = 6,36, P < .001) and of the interaction of colony pairs and observation period (sum of squares = 13,991.77, F = 2.75, df = 12,36,
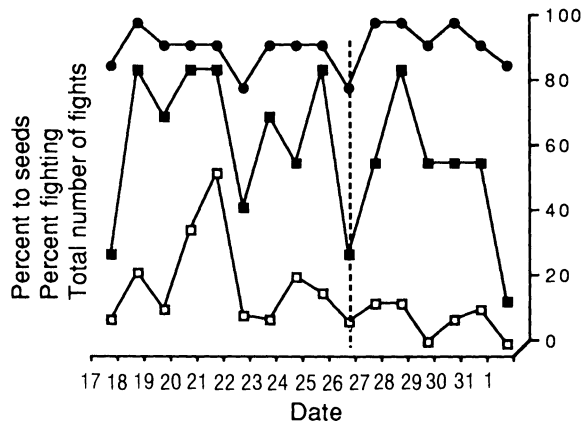
FIG. 8.—Response of adjacent pairs of colonies to artifical seed trails. *Filled circles,* percentage of 15 experimental colonies that foraged toward seed trails. *Filled squares,* percentage of experimental colonies that engaged in fighting. *Empty squares,* total number of fights between pairs of ants. Seeds were put out each day from July 17 to July 26. The vertical dotted line marks the first day that seeds were no longer offered.

$P < .05$). In three of the seven colony pairs there was a temporary reversal during one of the three time periods of the usual difference between the pairs. In these cases, weaker colonies foraged more than stronger ones during the first 3 d, or days 7–9, of the experiment. None of the other effects was statistically significant. The second ANOVA using observations between 9:30 and 11:30 A.M. had the same results. In general, stronger colonies continued to forage more than weaker ones, although food had been placed closer to weaker colonies.

Fighting took place in all experimental colonies. No fighting was observed in any of the pairs of unfed controls throughout the experiment. Figure 8 shows the total numbers of fights, and the proportion of experimental colonies that engaged in fighting each day. Fights took place between pairs of workers, who locked on to each other with their mandibles, and they often resulted in dismemberment and death. Almost all fighting took place within a region less than 1 m², a "fighting zone." By the fourth day of seed trails, a fighting zone had developed in all experimental pairs. In six of the seven experimental pairs this zone was much closer to the weaker colony; in one pair it was about halfway between the two colonies. The distance from each colony of the pair to the fighting zone was measured as a straight line along the route the ants were using to reach the area. The fighting zone was about a third of the way from the weaker to the stronger colony (mean distance, as a percentage of the total travelling distance between the two colonies, 30.1%, SD = 17.2).

Despite the fighting, both colonies in each experimental pair continued to collect the seeds. Thus, when aggression takes place, it does not deter the use of intersecting trails. In fact, both fighting and the use of intersecting trails continued for 7 d after seeds were no longer distributed. Fighting intensity was variable but decreased somewhat on the day that we stopped putting out seeds (fig. 8). By August 1, 7 d later, fighting had almost ended.

A colony's day-to-day decisions about where to forage depend both on food availability and on interactions with neighboring colonies. With an experimental food incentive, any pair of colonies can be induced to behave as undisturbed younger ones sometimes do: they engage in long-term conflict, in which fighting takes place but does not prevent the continued use of intersecting trails. In a conflict over food, the colony closer to the food does not appear to have any advantage.

The effect of colony age on the response of neighboring colonies to a new food source.—Observations described above suggest that interactions between neighboring colonies depend on colony age. To test this, a bait experiment was performed in 1989 with pairs of older (at least 5 yr) colonies and pairs of younger (2 yr) colonies. The experiment was performed twice, first with 10 pairs of each age group, and second, after an interval of 18 d, with nine of the same 10 pairs of each age group. On the day before each experiment, the trails of all colony pairs were mapped with a square grid of markers at 6.2-m (20-ft) intervals, large enough to cover the foraging trails of both colonies. The maps were accurate to about 0.5 m. These maps were used to find a line, equidistant from both nests of a pair, along which a seed bait was placed. The line was the shortest possible line connecting foraging trails of the two colonies, extending through an area in which no foragers of either colony were observed, and never less than 2 m from the nest entrance of either pair. On day 1 of the experiment, 8 g of seeds (about half the amount used in the experiment described in The Effect of Food Incentive, above) were scattered narrowly along this line. Seeds were distributed only on day 1 and not on subsequent days. On subsequent days (day 5 in experiment 1 and day 6 in experiment 2), the trails of all colonies were mapped each day, and all observations of fighting in two visits per day to each colony pair were recorded. In both experiments, all colonies foraged toward the bait and retrieved seeds on the day that seeds were offered. On subsequent days, trails from each of the two colonies toward and along the former line of seeds were considered to overlap if ants from each of the two colonies were observed within 30 cm of each other in 10 s. Because the same colony pairs were used in the second experiment as in the first, the two experiments should not be considered independent replicates. However, very heavy rain and flooding occurred during and after the first experiment. If ants placed pheromone markers on the soil during the first experiment, both the soil and the markers would have been washed away. Foraging activity and incidence of fighting were much higher in most undisturbed colonies during the rainy period of the first experiment than during the drier period of the second.

In both experiments, pairs of younger colonies used overlapping foraging trails toward and along the former line of seeds more often than older colonies. Figure 9 shows the time course of the results, representing, for each day, the number of older or younger colony pairs that foraged on overlapping trails and the number of pairs that fought. In the first experiment, after 7 d had elapsed since the day on which seeds were offered, most colonies of both age groups no longer foraged toward the site of the bait. In the second experiment, the use of overlapping trails declined but rose again on the sixth day.

The data were analyzed by application of a measure of the extent to which overlapping trails were used in each colony pair (not the day-to-day counts shown
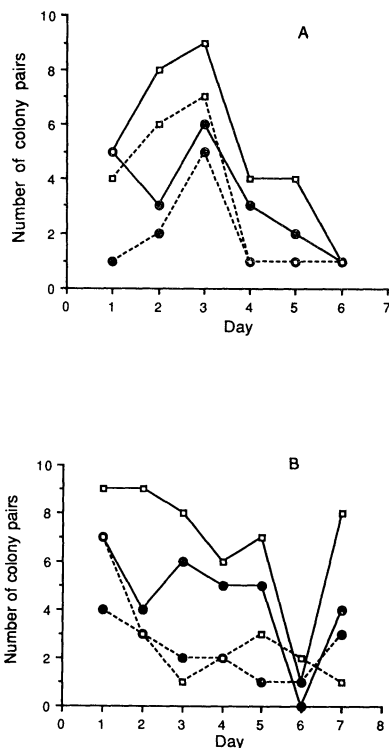
FIG. 9.—Comparison of older and younger colony pairs' response to artificial seed trails. A line of seeds was placed between foraging trails of an adjacent pair of colonies on day 1. The experiment was repeated after an interval of 18 d. *A,* Experiment 1; *B,* experiment 2. *Open squares,* younger (2 yr old) colonies; *filled circles,* older (at least 5 yr old) colonies; *solid lines,* use of overlapping foraging trails by both members of the pair, toward the former site of the seed bait; *dashed lines,* fighting at the former site of the seed bait. -

in fig. 9). For each colony pair, I found the proportion of days (out of 5 for experiment 1 and 6 for experiment 2), after the day bait was offered, on which foraging trails overlapped at the former site of the bait. Within each experiment, I compared the proportions in all older pairs with those in all younger pairs. Younger pairs were more likely than older ones to use overlapping trails in both experiments; proportions for younger pairs were higher (t-test [one-tailed]: experiment 1, $t = 1.77$, df $= 18$, $P < .05$; experiment 2, $t = 3.0$, df $= 16$, $P < .01$).

The observations of undisturbed colonies described above suggest that neighboring older colonies avoid trail intersections, whereas younger ones are more willing to engage in prolonged contact and fighting. The bait experiments described in this section confirm this. With a large food incentive (18 g of seeds/d), pairs of neighboring older colonies forage on intersecting trails, both while seeds are offered and afterward. With a smaller food incentive (8 g of seeds on a single day) younger colonies are more likely than older ones to forage on intersecting trails. A colony's day-to-day decisions about the location of foraging occur in the

context of long-term interactions with its neighbors. These decisions are influenced by food availability. The effect of food availability on interactions with neighbors depends on colony age.

Rate of Food Intake and Foraging Intensity

Flexibility of foraging is influenced by hour-to-hour changes in a colony's environment. Within a day, the rate of foraging seems to depend partly on the rate at which food is brought into the colony. In honey bees, this relation is a homeostatic one: when less food is brought in, foragers become more active (Seeley 1989). This does not appear to be the case in harvester ants. In previous experiments (Gordon 1986, 1987), barriers placed across foraging trails impeded, but did not stop, foragers returning to the nest with food. In response to barriers, colonies did not compensate for the obstruction by increasing the rate at which foragers left the nest; instead, the rate of foraging slowed further. This suggests that, in the course of a day's foraging activity, colonies modulate their foraging according to the rate of food intake, by foraging less when foraging is less successful.

To examine whether sharp decreases in food intake affect foraging activity within a day, I took away food items from foragers returning to the nest, and allowed the foragers themselves to return to the nest. Experiments were conducted for 2 d with six colonies, of which three were undisturbed. In the three experimental colonies, foragers returning to the nest with food were removed from the strongest foraging trail and deprived of the food they were carrying. Once deprived of their food item, foragers were held in a separate container so that they would become less alarmed. Within an hour (by 7:30 A.M., hour 2 in fig. 10), the foragers were returned to a second, less active foraging trail, so that counts on the original trail would not be affected by any alarm caused by the returned foragers. Returned foragers always went back into the nest. Removals began when foraging trails first showed substantial numbers returning to the nest and continued for 1 hr. During this hour, as many returning foragers as possible were removed and deprived of food, but it was never possible to remove the majority of foragers. Numbers removed ranged from 32 in a smaller colony on the second day, on which all colonies were less active, to 251 in a larger colony on the more active day. Each day, at 0.5-h intervals throughout the time that the colony was active, counts were made on each trail of the numbers of foragers passing a point on the trail (outside the site of removals and returns) in 20 s. Of 11 counts made each day, only the first two were directly affected by the removal and detention of foragers.

When returning foragers were deprived of food, the rate of foraging decreased (fig. 10). For each colony, I found the total of all counts of foraging rate. The first count, during which returning foragers were captured in experimental colonies, was omitted. The counts for experimental colonies were significantly lower than those for undisturbed ones (one-tailed t-test, $t = 2.143$, df $= 4$, $P < .05$).
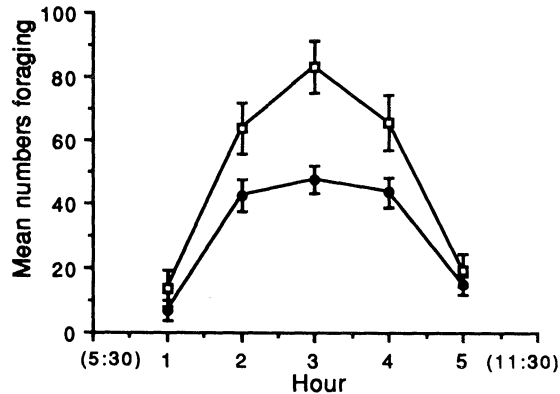
FIG. 10.—Effect on numbers foraging of depriving returning foragers of their food items. The graphs show the mean rates of foraging in three undisturbed colonies (*open squares*) and three in which food was taken from foragers (*filled circles*). Error bars show SEMs.

This result may be due to a combination of factors: a change in the rate of food intake or a short-term (<1 h) delay in the return of some foragers. To test this, a sham experiment was performed for one day with six other colonies in 1989. Three colonies were undisturbed. In three colonies, returning foragers were captured and later released exactly as above, but not deprived of their food items. All foragers were released carrying a food item. Foraging rates were counted as above. A delay in the return of successful foragers did not cause numbers foraging to decrease. There was no significant difference between undisturbed and sham experimental colonies in total numbers foraging on all trails (one-tailed t-test, $t = -0.096$, df $= 4$, $P < .46$).

A decrease in the rate at which successful foragers return to the nest causes a decrease in the rate of foraging. Thus, as previous experiments had suggested, the hour-to-hour dynamics of foraging intensity are not homeostatic in any simple way; that is, colonies do not immediately compensate for a decrease in food intake by sending out more foragers. Foraging trips outside the nest entail a cost to the colony in energy expenditure and in desiccation. It appears that when foraging becomes less profitable, colonies decrease the effort they expend on foraging that day. Does the intensity of foraging depend on the rate at which foragers return, the rate at which food accumulates, or the success rate of foragers? Most returning foragers are successful (mean percentage of foragers returning without food in six older colonies, 13.8, SD $= 12.66$). It may be that colonies make no functional distinction between the rate of flow into the nest of foragers and of food. Further experiments are needed to investigate this.

DISCUSSION

There has been a great deal of research on the foraging ecology of seed-eating ants, mostly concerned with two problems. One is the mechanisms and adaptive

value of the foraging behavior of individuals, and the characteristics, such as size and age, of the foragers themselves. A second is the factors, such as competition for food resources, contributing to demographic and evolutionary change at the population level. The work reported here is part of an attempt to bridge the gap between these two approaches. Interactions of neighboring colonies affect the retrieval of food. A colony's relation with its neighbors is influenced by the dynamics that determine, as conditions change, each colony's decisions about when, where, and how much to forage. Colonies consist of groups of workers, each of which carries out a different task. Interactions among worker groups within colonies determine the extent to which each task, including foraging, is accomplished in a particular situation. Thus the behavior of individual foragers can be understood only in the context of interactions among foragers and other worker groups within a colony, colony decisions about the intensity and location of foraging, and relations between neighboring colonies. In parallel, ecological variables such as survival rate and the distribution of nest sites depend on the flexibility of foraging behavior at the within-colony, colony, and between-colony levels.

Table 5 summarizes the behavioral flexibility of *Pogonomyrmex barbatus*. The table is organized into three columns representing the yearly, daily, and hourly time scales discussed here. The rows of the table correspond to three levels of organization. The bottom row refers to the behavior of groups of workers within a colony, each of which is devoted to a particular task. The middle row refers to colony-level behavior, such as decisions about whether, where, and how much the colony forages. The top row refers to interactions of neighboring colonies. The table summarizes both work reported in this study and previous work reported elsewhere. The discussion follows the table column by column, from the yearly to hourly time scales and, within columns, from bottom to top.

Within a colony, flexibility on the yearly time scale includes changes in colony organization as it grows older. A series of perturbation experiments were made to investigate interactions of worker groups within colonies (Gordon 1986, 1987). Perturbations included a disturbance increasing the numbers of patrollers and an alteration to the nest mound requiring extra nest maintenance work. Each directly affected only the numbers engaged in one activity. Each perturbation of one activity, such as nest maintenance, changed the numbers engaged in other tasks, such as foraging. This shows that different worker groups interact with each other, and these interactions affect the intensity of foraging. Perturbation experiments were performed in both older and younger colonies. The responses depended on colony age. Older colonies (>5 yr old) responded in a more consistent and more homeostatic way to disturbances than did younger ones (2 yr old). As the number and magnitude of perturbations were increased, the behavior of older colonies emphasized foraging more. Younger colonies, by contrast, allocated less effort to foraging and more to other tasks as perturbations increased.

These previous results suggest that, in a changing environment, older colonies are more stable, and in some sense better, foragers than younger ones. If colony mortality were higher among younger colonies, it could be argued that older colonies (>5 yr) are better foragers than younger ones (2 yr) because of current

TABLE 5

BEHAVIORAL FLEXIBILITY IN THE SEED-EATING ANT *POGONOMYRMEX BARBATUS*

LEVEL OF ORGANIZATION	TIME SCALE		
	Year to Year	Day to Day	Hour to Hour
Between colonies	Neighbor interactions are more stable and involve less conflict as colonies get older or as the duration of proximity increases	Level of aggression in neighbor interactions depends on food available; interactions are not deterred by fighting; once begun, conflict continues even after food is not available	Encounters with neighbors deter foraging*
Colony	Colony-specific differences in tendency to forage persist from one year to the next, but there is no simple relation of survival and tendency to forage	Colonies choose among a set of available trails; patrollers choose the day's foraging trails	Patrollers, not foragers, recruit other ants to retrieve food;† rate of food intake affects foraging intensity; when intake decreases, numbers foraging decrease
Task groups within a colony	Interactions among worker groups change as a colony gets older‡	Workers change tasks, and nonforagers become foragers if needed, but foragers do not change tasks;§ foragers change trails when recruitment is strong	Numbers foraging depend on events affecting workers in other tasks‖

NOTE.—The following refer to results not reported in this article.
* Gordon 1989*b*.
† Gordon 1983.
‡ Gordon 1987.
§ Gordon 1989*a*.
‖ Gordon 1986.

strong selection among younger colonies. In the extreme case, only the few younger colonies that behave like older ones would survive. The present results do not support this view. They show that colonies live to be 15 or 20 yr old, and there is no evidence of differential mortality between 2- and 5-yr-old colonies (table 1). Few of the young colonies previously studied have died so far. The rate at which sexuals are produced probably depends on colony age. The flexibility of foraging activity may affect reproductive success not through its effect on the survival rate but through an age-dependent effect on alate production.

At the colony level, there are colony-specific differences in behavioral flexibility that persist from one year to the next. Previous demographic studies (e.g., Davidson 1985) have shown that competition for food is strong. This has led some to explain the evolution of various aspects of the behavior of seed-eating ants by

assuming that any behavior that increases the rate of food acquisition would be selected for. If such selection is currently at work, one might expect colony variation in foraging activity to be highly correlated with colony variation in survival rate. I found no such relation. One of the ways in which a colony responds to environmental variability is by adjusting the intensity of foraging. Colonies vary in the ways they make such adjustments. From one year to the next, some colonies are consistently more likely to forage actively than others. But colonies more likely to forage actively are not more likely to survive to the next year.

A colony's need for food depends on its size and the amount of brood to be fed, both determined by colony age and queen fecundity. How much a colony must forage to survive is influenced by its current food requirements and by food availability. In a sample of 77 colonies over 3 yr, a general trend emerges. Long bouts of inactivity do not make a colony's food stores so low that its survival until the next year is threatened. This renders one puzzling aspect of previous results somewhat less puzzling: why colonies so readily decrease the numbers foraging in response to perturbations affecting other worker groups. For example, when the numbers doing nest maintenance are increased experimentally, foragers stay inside the nest (Gordon 1989a). It seems that the food deprivation caused by small decreases in foraging activity is not life threatening for the colony on the year-to-year time scale.

Interactions of neighboring colonies are flexible on the yearly scale, because the dynamics of such interactions depend on colony age (or size). Relations between a particular pair of neighbors depend on the duration of their status as neighbors. Workers distinguish between conspecific ants from neighboring and distant colonies (Gordon 1989b). The present study shows that relations among neighboring colonies vary with the ages of all colonies involved. Neighboring pairs of undisturbed young colonies were observed to stabilize in long-term conflict (fig. 7). Pairs of undisturbed older colonies were observed to avoid the use of intersecting foraging trails (fig. 6). Experiments showed that, with a large food incentive, even pairs of older colonies would use intersecting trails (fig. 8). With a smaller incentive, pairs of younger colonies were more likely than older ones to use overlapping trails (fig. 9).

Younger, smaller colonies may have smaller food stores than older ones, relative to the number of foragers available to retrieve food. Also, if younger colonies are rapidly increasing in size, the brood they must feed may be a larger proportion of the colony than the brood in older colonies, with correspondingly high nutritional requirements. For these reasons, younger, smaller colonies may be more willing to undergo conflict to obtain food.

On a yearly time scale, where a colony will forage, and how much, depends on its location. Its location determines the distance to food and the configuration of neighbors in which the colony is situated. Given its location with respect to neighbors and food, a colony's foraging decisions depend on its age. Colonies are long-lived, and changes in the distribution and ages of a colony's neighbors will have long-term effects. Contrary to predictions that competition should lead to overdispersed nest sites, the distribution of nest sites in the population studied

here changed from year to year and was either random or clumped (table 2). The distributions of desert annuals, whose seeds provide the main food source for harvester ants, also change on a year-to-year scale. The location of food sources, the dynamics of interactions among neighbors, and the ontogeny of these dynamics all affect competition for food and thus the relation between a colony's survival and the location of its nest.

On the daily time scale, within a colony, interactions among worker groups cause foraging to change. If, from one day to the next, there is a sudden increase in food availability, experiments with marked individuals reported here show that foragers will change trails to retrieve the new food source. In addition, previous work shows that ants from other task groups will switch tasks to forage if a new food source appears from one day to the next (Gordon 1989a). But foragers do not switch tasks when experiments cause numbers in other tasks to increase. Thus, the social organization of the colony channels workers into foraging from other tasks when they are needed, and once part of the foraging force, individuals tend not to leave it.

At the colony level, foraging trails are chosen each day from a set of available ones (figs. 2, 3). This decision is mediated by a distinct group of workers, the patrollers, each morning before the foragers are active (fig. 5). It seems reasonable that, on a given day, a colony's decision on whether to continue using a trail, and whether to allocate foragers to a new one, is affected by the amount of food coming in on existing trails. Experiments are under way to examine the effects of food quality and variability on such decisions.

On the day-to-day time scale, the location and intensity of foraging are affected by interactions with neighboring colonies. The extent of conflict depends on the ages of the colonies involved, as described above, and also on the amount of food available. Fighting does not prevent the continued overlap of foraging ranges that can go on for many days if the food incentive is sufficiently high.

Flexibility on the day-to-day time scale may help to explain why, as previous perturbation experiments showed, foraging is so readily decreased by events affecting other worker groups. Colonies seem to undergo cycles of foraging (fig. 1). On some days, after rains or for unknown reasons, numbers foraging are high in most colonies. After several days of intense foraging activity, foraging decreases, and colonies devote more effort to nest maintenance work. Nest maintenance may increase after a bout of intense foraging because the husks of seeds acquired are then carried out of the nest. Thus there is a day-to-day cycle involving bouts of foraging, then bouts of nest maintenance. Perturbation experiments showed a reciprocal relation between the intensities of nest maintenance and foraging: experiments that caused an increase in numbers doing nest maintenance caused a decrease in numbers foraging, and vice versa (Gordon 1987). It may be that experiments causing increases in numbers doing nest maintenance work are read by a colony as the end of a foraging period, so that foraging decreases. Similarly, experiments causing decreases in foraging may be read as the end of a foraging period, so that nest maintenance work increases.

Flexibility on the daily time scale reveals an interesting characteristic of harvester ant behavior: it is flexible but not fluid. If the dynamics of colony behavior

could be illustrated by the movement of points in a behavior space, they would resemble the dynamics of putty more than those of water. On the daily time scale, there is often a considerable lag in the response of a colony, and in the recovery from that response to the original or baseline condition. In other words, colonies seem to "remember" past disturbances and respond accordingly. (This aspect of colony behavior is not mentioned in table 5.) For example, experiments were conducted for 6 d in a group of older colonies, with perturbations causing significant differences between experimental and undisturbed colonies in the numbers of ants engaged in foraging and other activities. In the subsequent 6 d, no perturbations were inflicted, but the differences between undisturbed and experimental colonies persisted (Gordon 1986). In this sense, colonies are flexible, but the lag before recovery is long. When events cause a colony to bend into a new behavioral configuration, it takes a long time to bend back.

The seed experiments described here also show a lag in colony response on the day-to-day time scale. When seeds were placed near the trail of one of a pair of closely neighboring colonies, both colonies responded. New trails were formed toward the seeds, and both colonies engaged in extensive fighting. This behavior continued for 10 d after seeds were withdrawn (fig. 8). Having altered its behavior in response to a new food source, the colony will continue an apparently expensive and unproductive battle with a neighbor even when the food source is gone. This lag is more pronounced in younger colonies. Younger colonies were more likely than older ones to return to the former site of a seed bait, even though this meant encounters and sometimes fights with their neighbors (fig. 9). Age differences in this time lag may reflect the age differences in food requirements discussed above. When food sources are spatially rather stable, as are seeds growing on plants, it may be worth risking wasted foraging time to continue to return to a site where food was once plentiful. Younger colonies, with higher food requirements, may be more willing than older ones to undergo this risk.

A third example of a day-to-day lag concerns the tendency of patrollers to switch tasks (Gordon 1989a). In response to a new, abundant food source, patrollers switched tasks to forage. But this response varied, apparently depending on events of the preceding day. If the colony had first been exposed to an experimental disturbance requiring an increase in the numbers of patrollers, and a new food source was offered the next day, the patrollers were not likely to switch tasks to forage. If no disturbance had occurred the day before, patrollers switched to foraging when seeds were offered. In some sense, recently disturbed colonies appear to remember that more patrollers might be needed.

On an hour-to-hour time scale, the dynamics of harvester ant behavior show some rigidity. The daily round, a characteristic sequence of activities outside the nest, takes place each day despite interference from other species (Gordon 1988), disturbances (Gordon 1986, 1987), or light predation (Munger 1984; Gordon 1986). No matter what the disturbance, if a colony is active at all, nest maintenance and patrolling always precede foraging, even if this entails a sacrifice of available foraging time (Gordon 1988). Nest maintenance work may be necessary before foragers can leave the nest, and the scouting work of patrollers seems an essential preparation for foraging. But the intensity and temporal pattern of foraging itself

is flexible on the hourly time scale. Both are affected by changes in the numbers of nestmates engaged in nest maintenance or patrolling. Interspecific differences in the timing of foraging activity reflect competitive relations among many seed-eating species (Whitford and Ettershank 1975; Gordon 1984). We know little about how, on the hour-to-hour time scale, foraging intensity changes in response to interactions with other species.

At the colony level, the flexibility of foraging behavior changes from one hour to the next. A colony can respond to a new food source only if the patrollers find it early in the activity period (Gordon 1983). Later on in the day, foragers do not digress from an established trail to collect an abundant food source. But foragers do react to changes in food availability. Experiments described in this article show that, during the peak of foraging activity, when food intake decreases, so does the number of ants foraging (fig. 10). Previous results on task switching show that colonies are able to respond quickly to an increase in food supply, by allocating more foragers from other task groups to retrieve the new food sources. The present results show that colonies respond as well to a decrease in food intake; it may be unprofitable to expend foraging effort when food is not available.

Interactions of conspecific colonies cause foraging to change on the hourly time scale. Encounters with workers from neighboring colonies deter foraging within 40 min (Gordon 1989b). Encounters with workers from more distant colonies also deter foraging, but to a lesser extent. If neighboring colonies do use intersecting trails, this hour-to-hour deterrence effect may eventually cause them to avoid each other's trails from one day to the next. Foragers of older colonies were observed to avoid intersecting trails in the absence of any artificial food incentive (fig. 6). With a large, artificial food incentive, however, pairs of neighboring colonies immediately recruited foragers to go to the same site even when this entailed severe fighting (fig. 8). In undisturbed older colonies, it appears that the food to be gained on a trail shared with a neighbor is usually not worth the cost of territorial conflict.

Why have harvester ant colonies evolved the characteristic kinds of flexibility described here? In response to year-to-year environmental change in food sources and nest distribution, one might predict resilient behavior on long time scales (Levins 1968). On the other hand, because of competition for food and irregular bouts of seed production by desert annuals, colonies must respond to short-term changes in food availability. Storing large quantities of seeds creates a buffer between the colony and its environment. To understand the evolutionary ecology of desert communities, it will be necessary to learn more about the relation between environmental fluctuation and behavioral flexibility.

Various models have demonstrated ways in which persistent phenotypic plasticity may evolve (see, e.g., Via and Lande 1985; Houston et al. 1988; Maynard Smith 1988). Flexibility is usually modeled as a source of variation among individuals or populations. In other words, flexibility generates change through time, which may show up in an instantaneous measure as variation. For example, penguins can swim and walk, so if one specified the locations of some penguins, they would either be on the ground or in the water. Ducks are more flexible; they can swim, walk, and fly. Measures of the locations of ducks would show more

variation, because the latter could be on the ground, in the water, or in the air. If the evolution of flexibility is modeled from this perspective, then, to measure flexibility and test the models, one measures variation.

But behavioral patterns, like other phenotypic characters, can change on a variety of time scales and at several levels of social organization. The effects of such changes can ripple from one time scale to another, in ways that single, static measures of variation would not reveal. For example, flexibility in the daily activity rhythms of harvester ant colonies interacts with year-to-year, ontogenetic changes in colony behavior. Measures of variation among colonies, within a day, would be measures of the consequences of both day-to-day flexibility and year-to-year flexibility. But such measures would not reveal that the variation was caused by events on the day-to-day scale and on the year-to-year scale, each of which affect behavior. Moreover, instantaneous measures within a day could not show how events on the day-to-day or year-to-year time scales interact. Only measures that track colonies over time, in different conditions, can show how flexibility leads to variation, and how flexibility itself varies across colonies.

Complex patterns of behavioral change are part of the phenotype of many organisms. A challenge facing behavioral ecology is to find approaches to the study of flexibility that will render these patterns comprehensible. To learn how flexibility operates and how it varies, we must develop our ability to incorporate and connect changing patterns on different time scales and levels of organization.

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