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*Pogonomyrmex*

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## **Recruitment Behavior, Home Range Orientation and Territoriality in Harvester Ants, *Pogonomyrmex***

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**Summary.** 1. Scouts of the harvester ant *Pogonomyrmex barbatus*, *P. maricopa* and *P. rugosus* which discovered a new rich foraging area recruit nestmates by laying a trail with poison gland contents from the feeding site to the nest. Laboratory experiments have shown that *Pogonomyrmex* workers are stimulated to follow the trail by the trail pheromone alone.

2. The biological significance of the recruitment behavior was analyzed in the mesquite-acacia desert in Arizona-New Mexico, where the three species occur sympatrically. *P. maricopa* recruits less efficiently to food sources than does *P. barbatus* and *P. rugosus*. Generally the recruitment activity depends on a number of parameters of the food source, such as distance to the nest, density of the seed fall and size of the grains.

3. The recruitment activity is also affected by the presence, absence or distance of hostile neighboring colonies.

4. The use of chemically and visually marked trunk trails which originate from recruitment trails, guarantees and efficient partitioning of foraging grounds. It could be demonstrated that trunk trails, used by *P. barbatus* and *P. rugosus* during foraging and homing, have the effect of avoiding aggressive confrontations between neighboring colonies of the same species. They channel the mass of foragers of hostile neighboring nests into diverging directions, before each ant pursues its individual foraging exploration. This channeling subtly partitions the foraging grounds and allows a much denser nest spacing pattern than a foraging strategy without trunk trails, such as that employed by *P. maricopa*.

5. The behavioral mechanisms which maintain overdispersion both within and between species of *Pogonomyrmex* were investigated. Aggressive confrontations at the colony level and aggressive expulsion of foundress queens from the nest territories of mature colonies play thereby a major role. Observational as well as experimental data led to the conclusion that the farther away from its nest the intruder is, the less vigorous are the aggressive con-

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frontations with the defenders. Only when neighboring colonies are located too close together will increased aggressive interactions eventually lead to the emigration of the weaker colony.

6. *P. barbatus* and *P. rugosus* have a wide niche overlap, whereas *P. maricopa* seems to be more specialized in regard to food. This is consistent with the findings that interspecific territoriality between *P. barbatus* and *P. rugosus* is considerably more developed than between these species on the one side and *P. maricopa* on the other.

7. Although foundress queens, which venture into a territory of a conspecific mature colony are fiercely attacked, most of them are not injured, but rather dragged or carried to the territorial border and then released.

8. Nevertheless foraging areas, even of conspecific colonies, frequently overlap, but aggressive interactions there are usually less intense than at the core areas (trunk trails plus nest yards), which normally do not overlap and are vigorously defended.

## Introduction

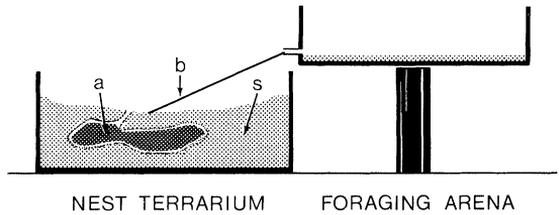
One of the most important reasons why ants are so successful ecologically is the great diversity of the social organization of the more than ten thousand species. Therefore, a fundamental understanding of the highly specialized adaptations of ants to many different ecological conditions must be constructed in large part out of the experimental analyses of social behavior and the communication signals that regulate this behavior. The evolution of many of these signals has been mediated by the selective force of intra- and interspecific competition.

Although considerable progress has been made in the analysis of the communication mechanisms (see reviews by Wilson, 1971; Hölldobler, 1973, 1975), relatively little attention has been given to the ecological implications of social behavior in ants (see reviews by Brian, 1965; Wilson, 1971). However, the biological significance of many social activities, such as recruitment behavior, or territorial behavior can only be understood by a combined behavioral and ecological analysis.

*Pogonomyrmex* is the most abundant and specialized genus of harvester ants in North America. The workers mainly collect seeds for food, but they also carry dead insects into their nests. In view of the great abundance of these ants in many parts of the United States (Cole, 1968) and their considerable ecological importance, surprisingly little has been learned to the present time concerning the ecology of their recruitment behavior to food sources (for review of relevant literature see Carroll and Janzen 1973), and the behavioral mechanisms which regulate territoriality and the partitioning of foraging grounds (Hölldobler, 1974).

## Material and Methods

Our study area was located in a mesquite-acacia community near the Southwestern Research Station (Portal, Arizona). This area is densely populated with nests of at least five *Pogonomyrmex*



**Fig. 1.** Laboratory nest arrangement.  
*a* nest; *b* bridge; *s* sand

species. We concentrated on three species, *P. barbatus*, *P. rugosus* and *P. maricopa*<sup>1</sup>, which seemed to have overlapping food preferences. For laboratory experiments colonies of these species were housed in sand filled terraria (75 × 30 × 30 cm). Each nest terrarium could be connected with a foraging arena 70 cm in diameter (Fig. 1). The latter combination provided an excellent arrangement for the pheromone tests and orientation experiments. The statistical evaluation was based on the Student's *t*-test and  $\chi^2$ -test. The null hypothesis was considered to be rejected when  $p < 0.05$ .

The investigations were conducted from 1969 through 1974 during the months of July and August. Additional methodological details will be given with the description of the individual experiments.

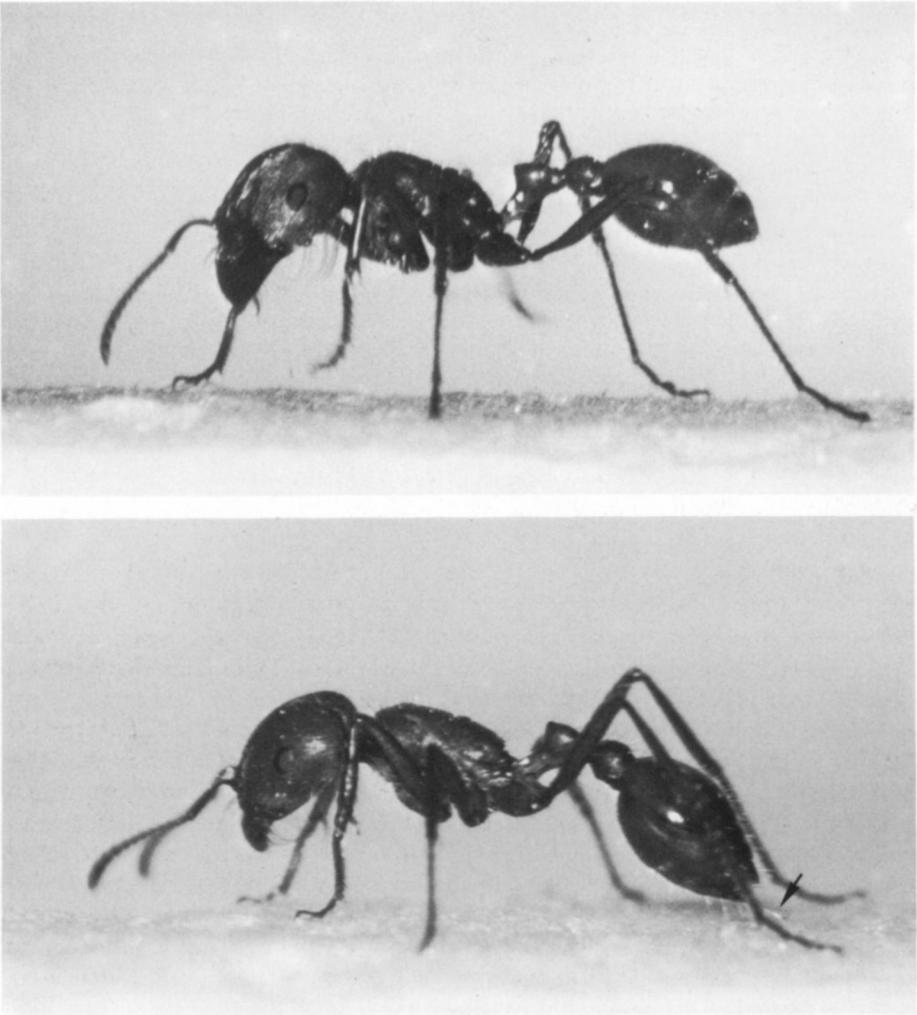
## Results

### 1. Recruitment Signals in *Pogonomyrmex*

Although in many ant species chemical trails laid down by worker ants are the essential signals for the initiation of mass foraging behavior in nestmates, they were not implicated or even suspected in *Pogonomyrmex* for many years. Since individual harvesting ants usually collect scattered seeds, casual observations in the past seemed to indicate a foraging system based on individual initiative and orientation.

In a laboratory study we showed for the first time that *Pogonomyrmex badius* uses recruitment pheromones released from the poison gland (Hölldobler and Wilson, 1971). Subsequent investigations demonstrated the same chemical recruitment behavior in 5 other *Pogonomyrmex* species, including *P. barbatus*, *P. maricopa* and *P. rugosus*. Many scout ants, after discovering a new rich food source (a new seedfall or a freshly killed cockroach) in the foraging arena (Fig. 1), return to the nest dragging the tip of the abdomen over the ground, often with the sting fully extruded (Fig. 2). Within seconds after the ant has entered the nest, nestmates almost invariably run out and take the precise course of the scouting ant over the bridge to the foraging arena. Our earlier results with *P. badius* strongly suggested that the other *Pogonomyrmex* species might use poison gland secretions as a recruitment pheromone. To test this hypothesis, the poison gland (with vesicles) and the Dufour's gland were first dissected out of workers of these species. For each replication the organs of a kind from 5 workers were washed in distilled water and then crushed in 0.2 ml benzine. Aliquots of 5  $\mu$ l of the benzine solution of the gland secretions were then applied with a syringe along the 50 cm long bridge which led from

<sup>1</sup> For confirming the identification of the species I would like to thank A.C. Cole.



**Fig. 2.** *Above:* *Pogonomyrmex maricopa* worker with the abdomen in ordinary position. *Below:* After discovering a rich source of food, the scouting ant returns to the nest, dragging the tip of the abdomen over the surface with the sting extruded (see arrow)

the nest entrance to the foraging arena. During the next 5 min a count was taken of all ants that passed over the bridge in the direction of the foraging arena. In control experiments counts were taken after pure benzene was applied. The data obtained (Table 1) show clearly that the poison gland has the strongest recruitment power. Dufour's gland secretions did not release a significant recruitment response. Although the laboratory studies demonstrated that *P. barbatus*, *P. maricopa* and *P. rugosus* use poison gland secretions as a recruitment pheromone, it was necessary to go to the field in order to analyze the biological significance of the recruitment behavior.

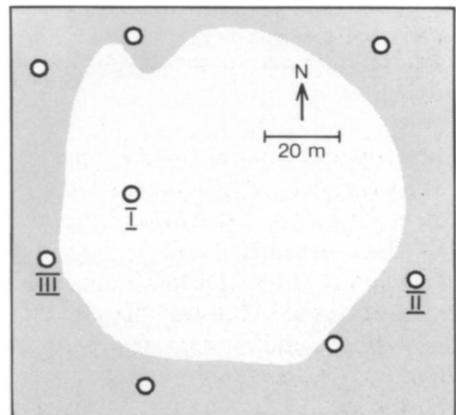
**Table 1.** Artificial trails composed of benzine solutions of different abdominal gland secretions were drawn for distances of 50 cm from the nest entrance. During the next 5 min all ants that followed the trails to the end were counted. Trails consisting of benzine alone were used as controls. The number of replications (N), the mean with standard deviation (M), and the range of the number of responding workers are given

	Control			Poison Gland			Control			Dufour's Gland		
	N	M	Range	N	M	Range	N	M	Range	N	M	Range
<i>P. barbatus</i>	8	9.4 ± 5.3	3-19	8	67.4 ± 32.6	21-120	5	7.8 ± 6.7	3-19	5	15.8 ± 9.0	7-29
<i>P. maricopa</i>	6	3.3 ± 4.5	0-12	6	43.3 ± 15.5	12-41	6	6.5 ± 3.9	0-10	6	8.3 ± 6.12	0-16
<i>P. rugosus</i>	5	4.6 ± 6.0	0-14	5	70.6 ± 31.54	39-111	5	9.8 ± 6.9	0-19	5	17.4 ± 9.5	4-30

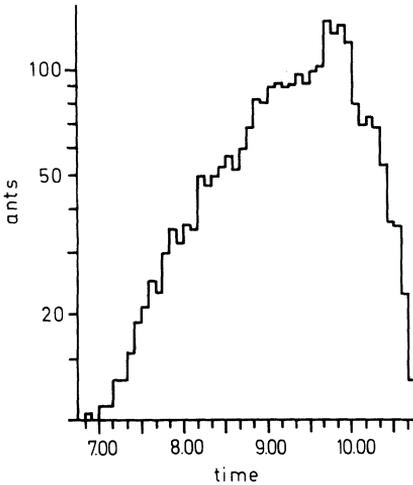
## 2. The Behavioral Ecology of Recruitment to Food

A preliminary survey indicated that *P. barbatus* and *P. rugosus* utilize the same food and nesting sites, whereas *P. maricopa* is somewhat more specialized on smaller seeds and tends to avoid nesting and foraging in areas where the vegetation is dense and relatively high. The daily activity rhythm of the three species in our study area proved very similar.

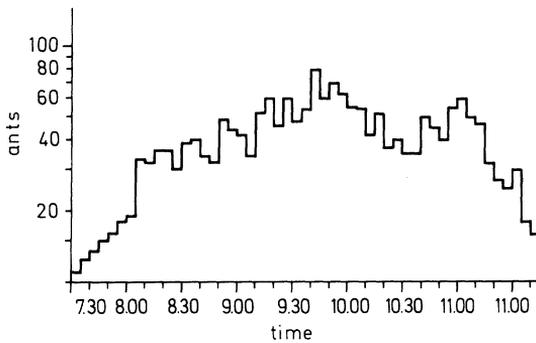
The first obvious question we had to answer was: Can recruitment be observed under field conditions? To conduct recruitment experiments in the field, we selected a *P. rugosus* colony (Fig. 3, Colony I) located in a large, plain and sandy area. One half of the nest surrounding (radius ca. 65 m) was almost completely free of vegetation. Most of the individual foraging excursions were directed to the other half, where a field of vegetation was located ca. 15 m from the nest (Fig. 3). The colony had no trunk trails. This situation resembled a huge foraging arena, where at least in one half of the arena we could control the availability of food. Before we provided seeds, we designated a feeding



**Fig. 3.** Array of *P. rugosus* nests on which recruitment experiments were conducted. Colony I was surrounded by a large sandy area. Screen = field of vegetation; o *P. rugosus* colonies



**Fig. 4.** Number of *P. rugosus* foragers arriving at a seed site 15 meters from the nest. Scores were taken in five minute intervals. Ordinate is here and in the following figures in logarithmic scale

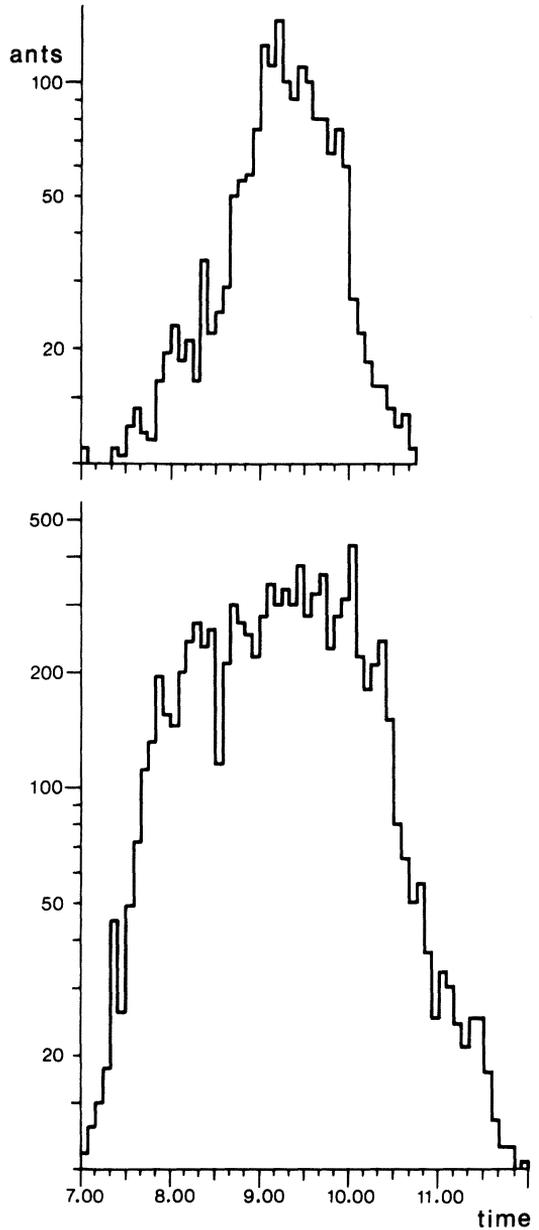


**Fig. 5.** Number of *P. maricopa* foragers arriving at a seed site (seed class 4, see Table 2) located 10 m away from the nest. Scores were taken in five-minute intervals

site, 20 × 20 cm on the ground and 15 m east from the nest entrance. In the following 20 min we counted all ants arriving at this spot during five-minute intervals. Then we filled the patch (densely packed) with seeds (seed # 3, see Table 2) and continued to count the arriving ants.

Soon after the first ants had discovered the seeds, they each picked up a grain and ran straight back to their nest. From this moment on, the number of ants arriving at the seed patch rapidly increased (Fig. 4). Although it is difficult in the field to observe trail laying behavior, movie film taken of individual foragers at high speed (70f/s) clearly demonstrated that many of them, especially those active at the beginning of the experiment, touched the abdominal tip on the ground, apparently laying a recruitment trail.

The foraging activity ceased almost abruptly at 10:45 a.m., when the surface temperature reached 46 °C. Although the recruitment response varied greatly with temperature and humidity, the basic recruitment response, illustrated in Fig. 4, was easily confirmed in all subsequent field experiments. Similar results were obtained with *P. barbatus*. Although *P. maricopa* foragers are only rarely seen to follow trails, this species also employs recruitment to food sources (Figs. 2, 5).



**Fig. 6.** Number of foragers of *P. rugosus* arriving at a seed site. Scores were taken during five-minute intervals. *Above*: seed site 45 m from the nest; *below*: seed site 10 m from the nest

The next question we asked was, how is the recruitment intensity affected by various parameters of the food source? In laboratory experiments we noted that different food sources elicit different recruitment responses. For example, a freshly killed cockroach usually caused a much stronger recruitment response than oat flakes in *P. badius*. Moreover, when all of the oat flakes were offered at one spot, the recruitment activity was more intense than if the same number

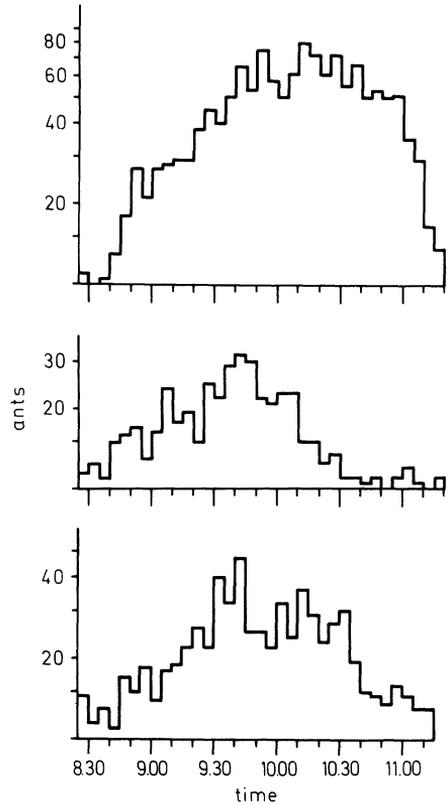
of flakes were scattered over the whole arena (Hölldobler and Wilson, 1970). The following account presents the results obtained from field experiments with *P. rugosus*. Basically similar results were obtained with *P. barbatus*.

First we tested whether the distance of the food source affects the recruitment activity. Using colony I (Fig. 3) again, we offered simultaneously in diverging directions ( $45^\circ$  apart) two seed patches ( $20 \times 20$  cm, seed #3, densely packed), one 10 m, the other 45 m away from the nest. As the data in Fig. 6 show, considerably more ants were recruited to the food source closer to the nest. Again the foraging activity declined at both feeding stations rather rapidly after about 10:00 a.m. (surface temp.  $47^\circ$  C), although it persisted for a longer period at the less distant seed patch. Six days later we conducted the same experiment with the same colony, although this time with reversed sides. Again the foraging activity was considerably higher at the more proximate site. Further experiments have shown that the effect is diminished when the difference between the distances of the feeding stations to the nest is decreased.

The weaker recruitment response to more distant food sources might be caused simply by the relatively high evaporation rate of the recruitment pheromone, causing newcomers to encounter more difficulty in finding the more distant food sources. In addition foragers need about nine minutes to return from the 45 m distant seed patch, whereas they travel only two min when they return from the 10 m food site to the nest. This means that about 4.5 more recruiters arrive at the nest in a given time from the 10 m site than from the 45 m site.

Not only the distance of the food source, but also the density of the seed fall can affect the recruitment response. This was shown by a series of experiments, the results of two of which will be discussed next. Two seed patches ( $25 \times 25$  cm) were provided in different directions, both 20 m distant from the nest but  $45^\circ$  apart. At both patches we offered the same seeds (seed #3, see Table 2). At one patch, however, the grains were densely packed, while at the other only 50 seeds were offered and these were evenly dispersed so that the grains were ca. 4 cm apart. In addition to these two patches a third patch was offered in which the seeds were widely dispersed as just described and only 10 m distant from the nest. At both these latter patches grains were continuously replaced as soon as foragers carried the seeds away. As can be seen from Fig. 7 the recruitment effect to the densely packed seed patch was considerably higher than to the other two seed patches, even though one of the latter was only 10 m away from the nest. A similar result is illustrated in Fig. 8 where we provided two seed patches ( $45^\circ$  apart) 25 m from the nest. At one, the grains were spaced ca. 2 cm apart, at the other they were 5 cm apart. The recruitment response was considerably higher to the more densely spaced seed patch. In 17 experiments conducted with *P. rugosus* and 9 experiments with *P. barbatus*, we offered two seed patches 25 m away from the nest but in different directions. In one the seeds were densely packed, while in the other the seeds were spaced (4 cm apart). In 12 of the *P. rugosus* tests and in 7 of the *P. barbatus* tests the recruitment response to the densely packed patch was significantly higher.

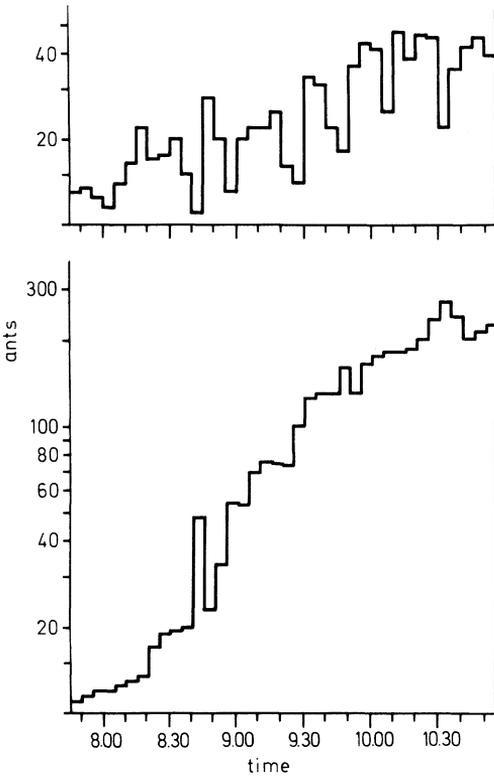
These results lead to the question of how the foragers measure the density



**Fig. 7.** Number of foragers of *P. rugosus* arriving at a seed site. Scores were taken during five-minute intervals. *Above*: feeding site 20 m from the nest; seeds densely packed. *Middle*: feeding site 20 m from the nest; seeds ca. 4 cm apart. *Below*: feeding site 10 m from the nest; seeds ca. 4 cm apart

of the seed fall. At this time it is only possible to speculate. It can be observed that individual foragers frequently do not take the first grain they encounter, but rather run around, touching several seeds until they finally pick up one and return to the nest. It is conceivable that during such a “probing” procedure the foragers get some sort of an input about the density and quality of the seed fall.

Frequently foragers can be observed to pick up a grain, let it fall, and then search for another one. This behavior could also provide them with information about weight and size of the seeds. Hence the next question we asked was: How does the size of the grains affect the recruitment activity? Table 2 shows the four size classes of grains we tested. The first experiments with *P. rugosus* clearly demonstrated a preference for a certain range of size classes. For example when we offered the same number of seeds of classes 1, 2 and 4 at the same patch 20 m from the *P. rugosus* nest, we found a distinct preference for class 4 (Fig. 9). To test whether this preference affects the recruitment activity, we provided grain class 4 at one site and grain class 1 at a second site. Both sites were located 20 m away from the nest and at a deviation of about 45°. The results were striking: the small seeds (class 4) elicited a high recruitment effect, whereas the foraging activity at the patch with the large seeds was low (Fig. 10). To be sure



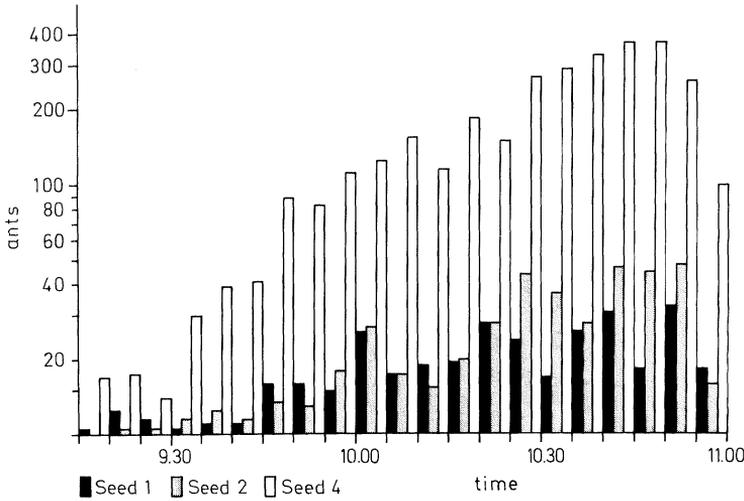
**Fig. 8.** Number of foragers of *P. rugosus* arriving at a seed site. Scores were taken during five-minute intervals. *Above:* feeding site 25 m from the nest; seeds ca. 5 cm apart. *Below:* feeding site 25 m from the nest; seeds ca. 1 cm apart

**Table 2.** The length (l) and width (w) of the four seed classes, measured in cm. Each measurement is based on 30 samples. Seed class 1=corn; seed class 2=wheat; seed class 3=parrot seeds; seed class 4=finch seeds

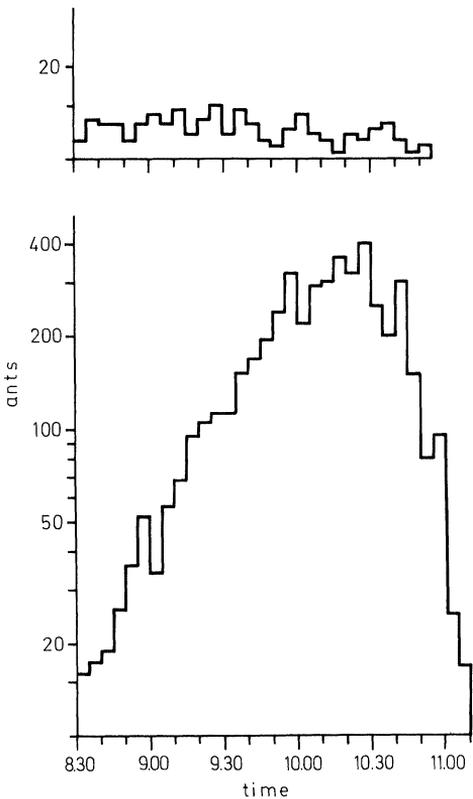
Seed	Class # 1	Seed	Class # 2	Seed	Class # 3	Seed	Class # 4
l	0.65 ± 0.16	l	0.63 ± 0.08	l	0.34 ± 0.08	l	0.21 ± 0.03
w	0.40 ± 0.07	w	0.25 ± 0.04	w	0.20 ± 0.03	w	0.11 ± 0.01

that this was not caused by a difference in quality of the seeds, we repeated the experiments, but this time we offered fragments of the large seeds about the size of the whole small seeds. The results were basically the same: the foraging activity at the smaller fragments was much higher than at the site with the large, whole grains.

In the next experimental series we compared two grain classes (3 and 4, see Table 2) which were not so markedly distinct, and no difference in the recruitment response was noted, even though *P. rugosus* showed a slight preference for grain class 3 when offered with other grain classes in the same patch. In several experiments we tested to see whether the large seeds (class 1) could



**Fig. 9.** Three different size classes of seeds (see Table 2) were offered at a feeding station 20 m from a *P. rugosus* nest. Scores of foragers, leaving the site with grains belonging to one of the size classes, were taken during five-minute intervals



**Fig. 10.** Two seed classes (see Table 2) were offered at two different feeding stations, each located 20 m from a *P. rugosus* nest. Above: number of foragers arriving at the feeding station with large seeds (class 1). Below: number of foragers arriving at the feeding station with small seeds (class 4)

become more attractive if offered closer to the nest entrance. In all cases (6 experiments) the recruitment to the smaller seeds (3 and 4) was higher, even if large seeds were offered as close as 4 m from the nest. However, once a foraging trail had been established, initiated by the offering of smaller seeds, the large seeds were also carried into the nest. This occurred over distances as great as 30 m; furthermore, the foraging activity did not decline markedly even after the small seeds were exhausted, provided we continued to feed large seeds.

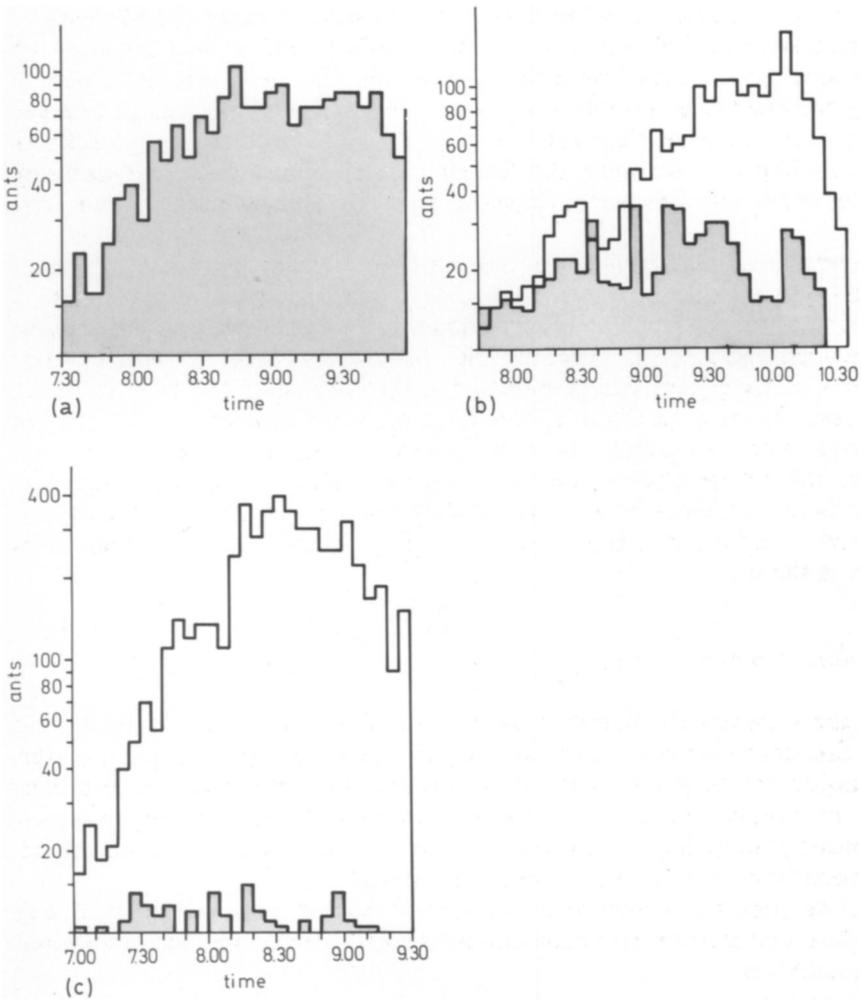
To summarize these results, it is clear that the recruitment activity depends at least indirectly on the distance of the food source, and it is affected by the density of the seed fall and by the grain size of the seeds. Similar results have been obtained for *P. barbatus*. No difference between *P. barbatus* and *P. rugosus* in their preference for certain grain sizes could be detected. Since *P. maricopa* shows generally a less intensive recruitment behavior, we did not get enough data to evaluate the same parameters in this species. We were, however, able to demonstrate that *P. maricopa* prefers the smallest grain size and clearly discriminates between size classes 3 and 4. Furthermore the recruitment activity rapidly declined when the feeding station was more than 20 m away from the nest.

### 3. Recruitment Behavior and Competition

During the experiments described above, we took care to avoid intra- and interspecific competition at the food sites. In the following account, however, consideration will be given to the effect on foraging activity by the presence, absence or distance of hostile intra- and interspecific neighboring colonies. Does a nearby competing colony decrease the "qualification" of a food source, in turn negatively affecting the recruitment intensity?

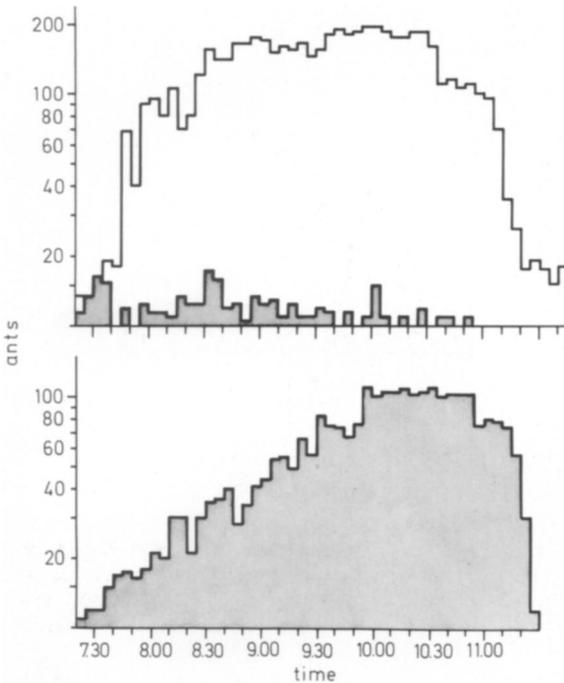
I will describe two experiments, conducted with *P. rugosus*, which clearly demonstrate that intraspecific competition strongly affects the recruitment and foraging activities.

In the first experiment a seed site (seed #3) was moved stepwise and eastward away from nest I (Fig. 3). After the second day it was taken to a distance of 45 m from the nest, but was still highly frequented by foragers. The site was now moved another 15 m away so that it was located 60 m from nest I; at this point it was closer to nest II, which was 30 m away. Since the foragers of colony I had already established a track in the direction of the food source, it is not surprising that they quickly discovered the 60 m site and the foraging activity was renewed (Fig. 11a). However, 35 min after this food source was set up, the first scouts of nest II apparently arrived at the site as well, because brief fighting was observed and a few ants carried seeds away in the direction of nest II. Now the number of ants arriving from nest II increased. However, the maximum rate was not more than 12 ants in 5 min, whereas 90 foragers arrived from nest I during the same interval. Throughout the observational period we saw periodic fighting, but generally the situation did not alter until the foraging activity ceased. The next day we again provided seeds at the 60 m site. Now the situation changed markedly: nest II rapidly built up a foraging force, whereas the activity of nest I was greatly reduced (Fig. 11b). Only relatively few fights could be observed, and most of them occurred in the first hour. Finally, in subsequent days the food site was completely controlled by foragers of colony II, and only very few foragers of colony I were noted in the vicinity (Fig. 11c). Most of the ants leaving nest I in the direction of the food site did not run further than 40–45 m.



**Fig. 11a-c.** A feeding station with seeds (class 3) was moved stepwise to the east away from colony I (see Fig. 3), until it was 60 m from colony I and 30 m from colony II. (a) During the first day foragers arriving from nest I were clearly dominant at the feeding station. (b) On the second day considerably more foragers from nest II (white) arrived at the feeding station, whereas the number of foragers of nest I (screen) decreased. (c) On the third day foragers of nest II were completely dominant at the feeding station

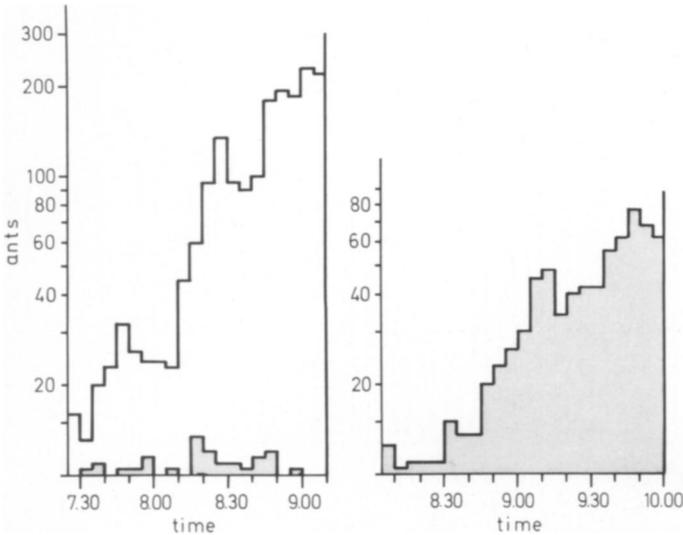
For the second experimental series we offered two food sites in different directions. One site, located 30 m southeast from nest I (Fig. 3), was relatively isolated and was chosen to avoid competition from scouts of neighboring colonies. When we occasionally noted an ant from another colony at this site, the forager was immediately eliminated. The second seed site was located 25 m southwest from nest I, and 6 m east from nest III. Thus competition at this site was expected to be high. As Fig. 12 shows, foragers of colony I rapidly built up a foraging force at the first feeding station, whereas the second feeding station was controlled by colony III.



**Fig. 12.** Two feeding stations were provided simultaneously. *Above*: station was located 6 m from nest III and 25 m from nest I (see Fig. 3). Foragers of nest III (white) clearly dominated over foragers of nest I (screen). *Below*: at the second (control) station, 30 m from nest I, foragers of nest I built up a strong foraging force (screen), since they had no competition from a neighboring colony

Five parallel experiments conducted on *P. rugosus* and three experiments on *P. barbatus* produced basically the same results. Generally the nest closest to the food source proved more successful in recruiting a forager force which then led to the exclusion of foragers from other nests. If, however, the food site was more than 30 m away from both colonies, a different situation arose. In a total of 8 experiments (conducted with three different pairs of colonies of *P. rugosus*) foragers of both nests frequented the isolated food source for several days. In these cases, neither colony built up a considerable foraging force and the aggressive encounters were mostly rather short-lived. The foragers showed more avoidance behavior than open aggression.

The interspecific competition for food sources between *P. rugosus* and *P. barbatus* was similar to the intraspecific competition within these species. In most of the experiments either the one or the other species dominated at the food source, and the decisive factor between equally large colonies was the proximity to the food source. This relation can be illustrated with the following typical experiment. A food site (seed class 3) was set up 12 m from a *P. rugosus* nest and 25 m from a *P. barbatus* nest. No trunk trail from either nest previously led in the direction of the food site. Although scouts from both nests arrived

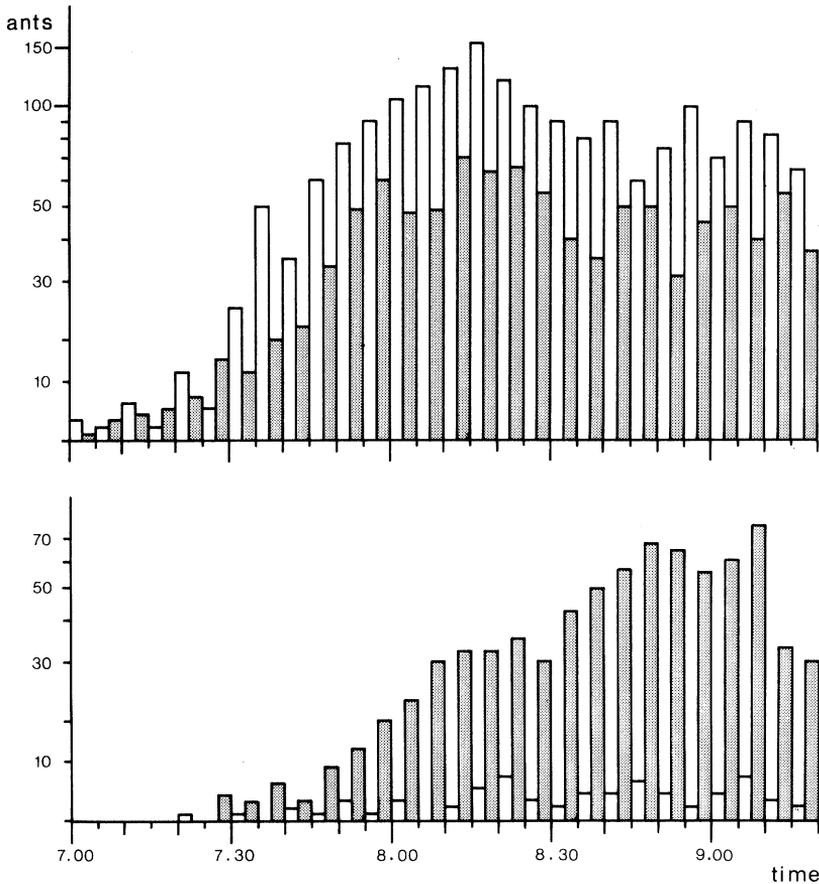


**Fig. 13.** A foraging station was located 12 m from a *P. rugosus* nest and 25 m from a *P. barbatus* nest. *Left*: *P. rugosus* (white) showed a more vigorous recruitment activity and dominated *P. barbatus* foragers at the nest site (screen). *Right*: two days after the *P. rugosus* colony was experimentally excluded, the *P. barbatus* colony built up a considerable foraging force at the feeding station

at the seed patch, *P. rugosus* showed a more vigorous recruitment response and soon dominated the food site completely. The next day we prevented *P. rugosus* from visiting the food source, and two days later *P. barbatus* had built up a considerable foraging force at the seed site (Fig. 13).

Quite different results were obtained in competition experiments between *P. maricopa* and either *P. barbatus* or *P. rugosus*. In all experiments *P. maricopa* coexisted at the food sites with these other two species, although its recruitment response was usually weaker. One experiment, illustrated in Fig. 14, is representative of 7 replications. Seeds of the grain classes 3 and 4 were offered at the same site ( $50 \times 50$  cm) 15 m away from a *P. maricopa* and *P. rugosus* nest. Workers of both species recruited nestmates to the food site. Although the recruitment response of *P. maricopa* was weaker than that of *P. rugosus*, both species frequented the site throughout the experimental period. It also became obvious again in these experiments that *P. maricopa* preferred the smaller seeds (class 4), whereas *P. rugosus* showed a slight preference for the larger grains (class 3). Although aggressive encounters were not very frequent during foraging, the intensity of fighting increased when the food supply began to decline. Under these circumstances *P. maricopa* seemed to be the more active aggressor.

In summary, recruitment of nestmates plays a major role in the foraging strategy of *Pogonomyrmex*. The ecological significance of the recruitment behavior becomes especially clear when placed in the context of the strong competition and territoriality of these harvesting ants. Those colonies able to recruit most efficiently to new seed falls usually succeed in being the dominant forager at the food site.



**Fig. 14.** A foraging station was located 15 m from a nest of *P. maricopa* and a nest of *P. rugosus*. Approximately equal numbers of seeds of classes 3 and 4 (Table 2) were offered. Both *Pogonomyrmex* species recruited nestmates to the feeding station. Scores of ants, carrying back either the large (white) or small seeds (screen) were taken for each species. *Above: P. rugosus; below: P. maricopa*

#### 4. The Significance of Trunk Trails in the Foraging System of *Pogonomyrmex*

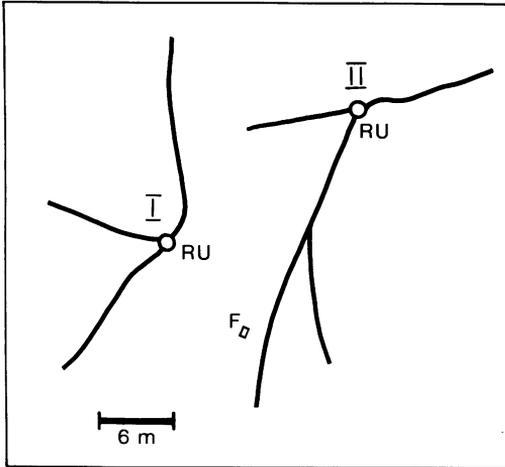
A striking etho-ecological difference between *P. barbatus* and *P. rugosus* on the one hand and *P. maricopa* on the other is that in the latter species individual foragers usually leave the nest in all directions, whereas in many of the *P. barbatus* and *P. rugosus* colonies most of the foragers travel on well established trunk trails before diverging on individual excursions (Hölldobler, 1974). After foraging, the *P. barbatus* and *P. rugosus* workers return to these routes for homing. Such trunk trails sometimes extend for more than 40 m; they are remarkably persistent over long periods of time and even survive heavy rainfalls (Fig. 15). As the following experiments will show, the trunk trail system plays a major role in extending the foraging and recruitment ranges of *P. barbatus* and *P. rugosus*.



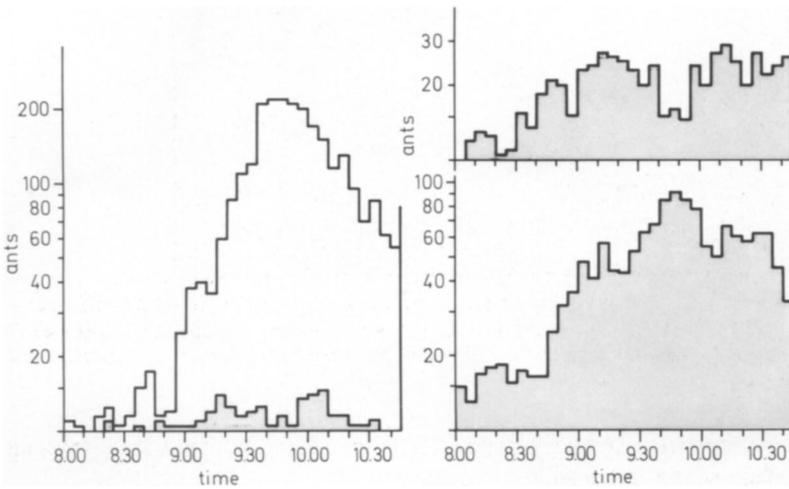
**Fig. 15.** Photograph showing a *P. rugosus* nest (*N*) with two distinct trunk trails (*T*)

In the recruitment experiments discussed so far, we either selected colonies, which had no trunk trails, or else the food site was set up in a cleared area, in which no trail system was established. In these cases it was seen that the nest most proximate to the food source usually builds up its foraging force more efficiently than more distant colonies. If, however, the food source is located relatively close to a trunk trail belonging to a more distant colony, this colony has a good chance of being more successful at exploiting the new food site than the more proximate colony. This was demonstrated in six replications of an experiment; the results of a typical replication will now be described in more detail.

We provided a food source (seed class 3, on a patch  $50 \times 50$  cm) at a site 10 m from nest I and 20 m from nest II (both *P. rugosus*) (Fig. 16). A trunk

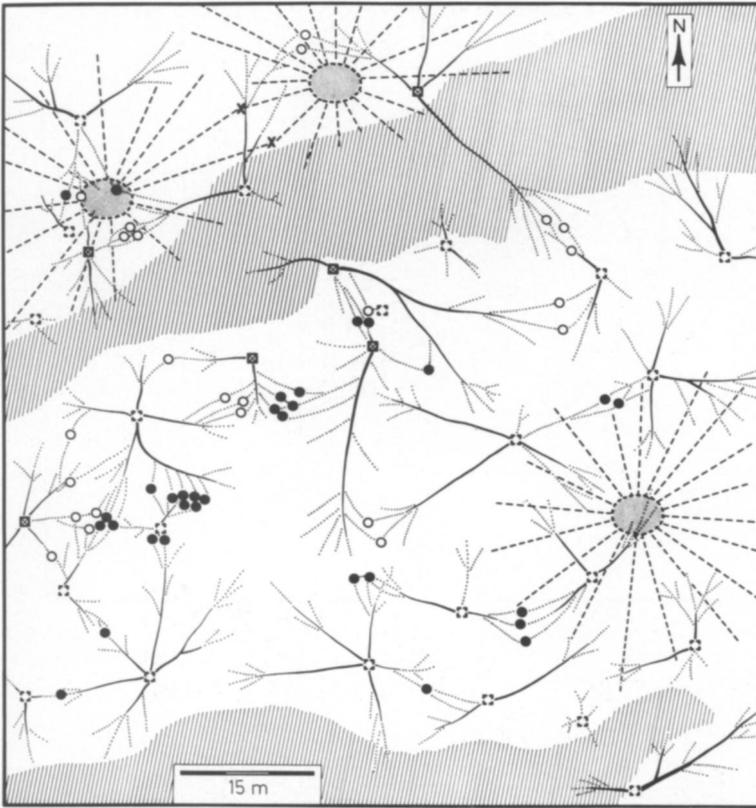


**Fig. 16.** The nest sites and trunk trails of two neighboring *P. rugosus* nests. A feeding station (*F*) was set up close to a track of colony Ru II. For further explanation see text



**Fig. 17.** Recruitment activity of foragers of two *P. rugosus* colonies to the feeding station illustrated in Fig. 16. *Left:* foragers of colony Ru II (white) dominate their competitors at the feeding station. *Right, above:* three days after colony Ru II has been excavated and removed, colony Ru I began to build up a forager force at the feeding station. Recruitment activity of Ru I increased even more after the fourth day (below)

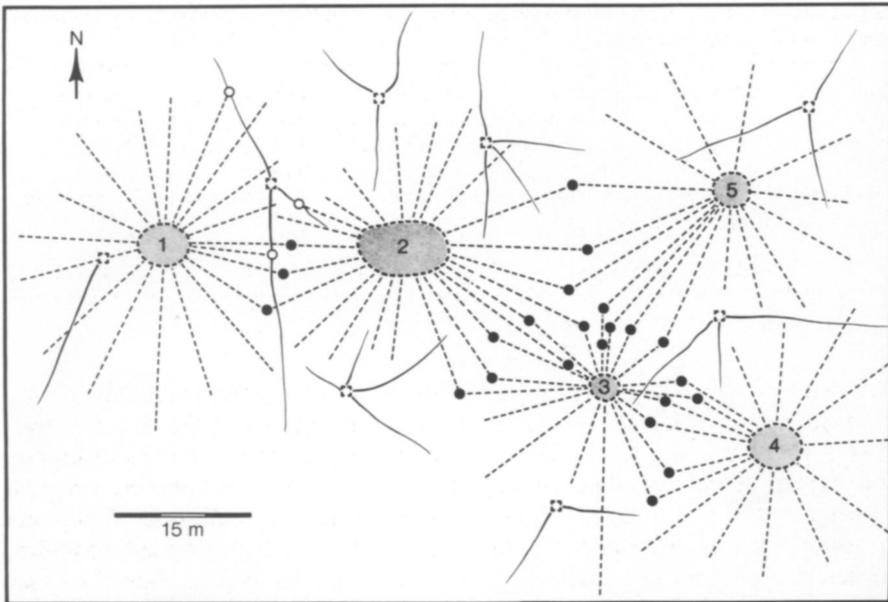
trail of nest II passed the experimental food site only 1.5 m away. As the data in Fig. 17 show, foragers of nest II first discovered the patch with seeds and rapidly recruited nestmates from the trunk trail to the site. In the following days we continued to provide seeds at the same patch, but eliminated foragers of nest II by excavating the whole colony. After only 3 days foragers of nest I started to recruit nestmates and finally, on the fourth day, a strong foraging force of nest I built up at the experimental food site (Fig. 17). This experiment demonstrates, as have three others of similar design conducted with *P. rugosus*



**Fig. 18.** Map of the colonies and their foraging areas in one section of the study site in Arizona. ● *P. maricopa*; ■ *P. rugosus*; ✕ *P. barbatus*; // higher grass vegetation; ● intraspecific fighting *P. rugosus* or *P. barbatus*; ○ interspecific fighting *P. rugosus*/*P. barbatus*; ✕ intraspecific fighting *P. maricopa*

and two with *P. barbatus*, that the trunk trails in effect partition the foraging grounds between competing colonies.

Employing a cartographic survey in two sections of our study area, we compared spacing patterns, foraging ranges and trunk trails of the three species (*P. barbatus*, *P. rugosus* and *P. maricopa*) (Figs. 18, 19). The following conclusions and inferences were drawn. (1) Trunk trails of intraspecific neighboring nests never cross. On the contrary, they regularly diverge as though the trail laying workers had been repulsed from pre-existing trails. (2) When workers leave the track and disperse on individual seed collecting trips, they occasionally meet workers of intraspecific neighboring colonies. This frequently leads to fierce fighting which can end with severe injury of even death. Such encounters usually occur only between pairs of ants. Mass confrontations are evidently avoided by the divergence of the trunk trails. (3) Trunk trails of interspecific neighbors (*P. barbatus* and *P. rugosus*) are usually also clearly separated. Individual encounters between *P. barbatus* and *P. rugosus* are as aggressive as intraspecific encounters. (4) *P. maricopa* has no trunk trails. Individual workers



**Fig. 19.** Map of relatively closely spaced *P. maricopa* colonies and their intraspecific fighting zones. *P. rugosus* nests in the immediate neighborhood are also indicated. ● intraspecific fighting, *P. maricopa*; ○ interspecific fighting *P. maricopa*/*P. rugosus*

forage out up to 25 m in all directions around the nest. They run across the tracks and even the nests of *P. barbatus* and *P. rugosus*. Individual interspecific aggressive encounters between *P. maricopa* and the other *Pogonomyrmex* species usually last only a few seconds and only rarely end fatally. However, when *P. maricopa* workers meet at the borders of foraging ranges of their respective colonies, prolonged heavy fighting can occur. As can be seen from Fig. 19 such fighting zones are especially active when a younger colony (Fig. 19, nest No. 3) is gradually growing and extending its territory between already established territories of the three other colonies (nest Nos. 2, 4, 5). It is apparent in the case shown that colony No. 3 will eventually be pushed out of its presently occupied nesting and foraging area. Indeed in a survey conducted one year later, this colony was found 9 m away from its former location. (5) The lack of a trunk trail system apparently forces *P. maricopa* to space out over much larger distances than *P. barbatus* and *P. rugosus* do (Table 3). Trunk trails appear to be devices to avoid intraspecific aggressive mass confrontations between neighbouring colonies. They channel the mass of foragers of hostile neighbouring colonies into departing directions, before each ant begins to explore on its own. This foraging technique ensures a more effective partitioning of foraging grounds and allows a much denser nest spacing pattern than the foraging strategy employed by *P. maricopa*. It is probably significant that in very dense populations of *P. barbatus* and *P. rugosus* the trunk trail system is considerably more elaborate than in sparser populations.

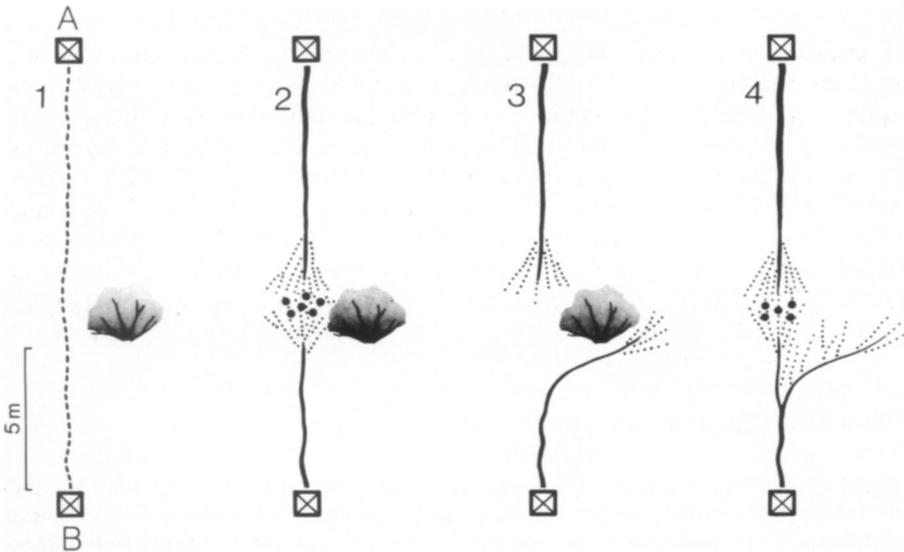
**Table 3.** Mean distances to nearest neighbors (in meters, with standard deviation) among *P. barbatus*, *P. rugosus* and *P. maricopa* nests

Distance between <i>P. barbatus</i> and <i>P. barbatus</i>	Distance between <i>P. rugosus</i> and <i>P. rugosus</i>	Distance between <i>P. maricopa</i> and <i>P. maricopa</i>	Distance between <i>P. barbatus</i> and <i>P. rugosus</i>	Distance between <i>P. barbatus</i> and <i>P. maricopa</i>	Distance between <i>P. rugosus</i> and <i>P. maricopa</i>
<i>n</i> = 35	<i>n</i> = 55	<i>n</i> = 66	<i>n</i> = 38	<i>n</i> = 21	<i>n</i> = 58
18.1 ± 5.3	19.4 ± 5.8	45.6 ± 25.5	17.4 ± 6.2	11.9 ± 6.5	14.1 ± 5.6

We next asked how trunk trails are established in the first place. Our recruitment experiments in the laboratory and in the field suggested that they originate at least in part from former recruitment trails. For example, when food sources were provided over a period of 3–4 days or longer the ants established a regular route between the nest and the food site. In *P. barbatus* as well as in *P. rugosus*, these routes frequently were maintained even after we had stopped providing more seeds. Foragers left the nest along these tracks before they dispersed for their individual foraging excursions and they returned to the tracks for homing. Thus the recruitment trail became a trunk trail. Also, laboratory experiments showed that in addition to the relatively short lived recruitment pheromone, more enduring chemical signposts are deposited along the trails (Hölldobler and Wilson, 1970). The latter substances function as orientation cues (Hölldobler, 1971), so that even when the recruitment signal has long since evaporated, motivated foragers are still able to follow the same track.

The hypothesis that the design of the trunk trail system is affected by the competition and territorial behavior of neighboring colonies has already been strongly supported by the results of the recruitment experiments, discussed above. I will now describe one representative experiment which demonstrates that the trunk trails can indeed function as orientation channels for the masses of foragers to ensure an efficient partitioning of foraging grounds with a minimum of hostile confrontations with neighboring colonies.

We laid a “seed line” between two closely neighboring colonies of *P. barbatus* (Fig. 20). Workers of both nests soon began to carry the seeds into their own nest; thus the line began to be “rolled up” almost simultaneously from both ends. When the two foraging groups met we continued to provide seeds at the meeting point. This kept the foraging activity going from both sides and led finally to heavy conflict. Within the next 4 hrs we counted 214 fighting ants. Even after the daily foraging activity had ceased, ants were still fiercely tangled together. During the next two days we continued to provide seeds in this fighting zone. The battles continued, even after we stopped providing seeds. After three days we had collected 311 killed ants, at which time the termini of the trunk trails were seen to be diverging. Colony A (Fig. 20) still used the newly established trunk trail, whereas colony B bent its route about 40° to the west. We conducted a total of 32 similar experiments with *P. barbatus* and *P. rugosus*. No differences in the forms of intraspecific conflict could be



**Fig. 20.** Schematic illustration of a field experiment demonstrating that trunk trails are established as an outcome of the recruitment process. (1) Two nests of *P. barbatus* (A and B) were connected by a line of seeds. (2) After foragers of both nests carried in the seeds, they finally met. When we continued to offer seeds at the contact site, heavy fighting developed between workers of A and B (●). (3) After we stopped providing seeds, the track began to diverge. (4) By removing a conspicuous landmark (bush) it was found that the change in the course of track B had been stabilized by this landmark

noted between these two species. In seven cases the opposing trunk trails diverged, in 20 cases only one colony withdrew, and in five cases both colonies withdrew completely from the newly established trunk trails. By changing topographical cues along the trunk trails we could demonstrate that visual markers (such as bushes, etc.) are responsible for stabilizing such course changes of trunk trails. This can be illustrated with the striking example in Fig. 20. Before separation of the colliding trunk trails the route of colony B passed a bush on the left side. After the course of the track had been changed it passed the bush on the right side. However, when the bush was removed, the course of the track of colony B became less accurate and aggressive confrontation with ants on track A increased again considerably. From this we can conclude that the chemical signals along the trunk trails are supported by visual cues, such as conspicuous, nearby landmarks. This, of course, requires that the ants acquire an intimate familiarity with these visual cues in the course of following the chemical trails. The next experiments, therefore, were designed to investigate the trunk-trail fidelity of foragers and the home range orientation in *Pogonomyrmex* in general.

### 5. Home Range Orientation and Route Fidelity

Topographic orientation in ants has been extensively studied by many investigators. Most of this work has been concerned with the behavioral and sensory

physiology of visual orientation and less with the ecological implications (Brun, 1914; Jander, 1957, Voss, 1967; Kiepenheuer, 1968; and others). Only recently have investigations concentrated on the ecology of home range orientation. Wehner and Menzel (1969) and Wehner and his associates (see literature in Wehner, 1972) conducted an extensive study on ecological factors regulating the homing orientation of *Cataglyphis bicolor* and Rosengren (1971) has investigated the route fidelity and visual orientation in several species of the genus *Formica*. Very little is known about the orientation behavior of *Pogonomyrmex* (Holldobler 1971). Because *Pogonomyrmex* is highly territorial a precise home range orientation seems to be an essential adaptation on the part of foraging workers.

#### a) Trunk Trail Fidelity of *P. barbatus* and *P. rugosus*

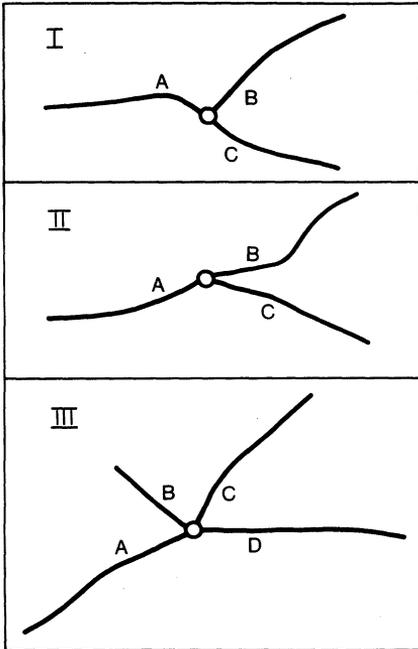
(1) Experiment: A large colony of *P. barbatus* which had 3 distinct trunk trails (Fig. 21-1) was selected. On trunk trail A, 425 foragers were individually marked with a yellow spot (PLA paints) and 450 foragers on trail C were marked with a blue spot. During the next ten days each track was searched almost daily for marked ants. During three searching periods in the morning and afternoon (lasting ca. 10 min), each track was examined and the marked ants were captured and counted. After each check the marked ants were released again on the track. As Table 4 shows, by far the most marked ants were found on the track where they had been marked. In a similar experiment, previously conducted with *P. barbatus*, only 5 ants out of 400 marked on one trunk trail were seen during the next three weeks leaving the nest on another track.

(2) Experiment: A large colony of *P. rugosus* with three trunk trails (Fig. 21-II) was selected. Three hundred foragers each on route A and route C were marked with a yellow and a blue spot, respectively. Counts of marked ants captured on the tracks were taken on four different days, as described above. As shown in Table 5 most of the captured marked ants were found on the track where they had been marked. Surprisingly, however, a relatively large number of ants deviated from route C to route B. One of the reasons for this might be that routes B and C were not very far apart. Another reason, however, might be that the number of foragers on track B increased generally, perhaps due to a recruitment effort of original foragers on route B. Indeed, in one experiment, described next, we were able to establish that the distribution of foragers on the trunk trails can be affected by a local change in availability of food.

(3) Experiment: At one *P. rugosus* nest with four distinct trunk trails (Fig. 21-III) we marked 500 foragers on track A. During the next three days all four routes were repeatedly checked (as described above) and all marked ants counted. Table 6 gives the mean number of rediscovered ants during a total of 10 inspections for each trunk trail conducted during the following day (each inspection lasted 10 min). After two days a rich food source (seed class 4) was offered at the end of route D (Fig. 21). We soon recognized that the number of marked ants increased on route D. Although one day later most of the marked ants were still captured on track A, the number of marked ants found on track D had significantly increased (Table 6). This clearly suggests that foragers can be directed from "their" trunk trail to another one, providing a stronger forager force is needed there. Most likely this flexibility is achieved by the chemical recruitment system.

#### b) Orientation on the Trunk Trail

The pilot experiments related above showing the high degree of trunk trail fidelity suggest that visual markers play a significant role in the recognition of specific trunk trails by foragers. Since we noted that the ants used the observer, who



**Fig. 21.** Topography of trunk trails of 3 *Pogonomyrmex* nests are shown which were used to test the route fidelity of foragers (see Tables 4, 5, 6)

was sitting at the food patch, as a visual landmark in locating the seed site during various experiments, we first tested to what extent specific visual markers are used in addition to the chemical signals for orientation on foraging trails.

In a cleared area (no bushes, etc.) a seed site 25×25 cm (seed class 3) was set up 30 m away from a *P. rugosus* nest. A black cardboard disk (100×75 cm) was positioned 1 m from the seed patch, facing toward the nest. The number of ants returning to the nest from the seed site was counted in five-minute intervals. After a foraging period of 2.5 hrs, the cardboard disk was moved 2.5 m to the side. Many of the arriving ants shifted their course toward the new position of the visual marker when they were about 2–3 m away from the seed patch, and they searched near the landmark for the food. During the next 15 min a smaller number of ants arrived at the seed site; consequently the number of returning foragers at the nest entrance decreased considerably, from  $114.2 \pm 11.3/5$  min to  $53.7 \pm 38.5/5$  min ( $n=6$ ). After we had returned the visual marker to its original position, the distracted ants quickly oriented back to the seed site and the number of returning foragers increased again. Similar results were obtained when the landmark was moved to a distance of 10 m from the nest. Many of the outward bound foragers did not continue on their way to the food source, but instead searched near the landmark. Consequently in the next 15 minutes the number of foragers returning to the nest decreased significantly from  $103.5 \pm 21.6/5$  min to  $33.7 \pm 11.2/5$  min ( $n=6$ ). When the landmark was removed completely, the ants ran along the route to the seed patch. However, we noted that the ants had greater difficulty in locating the food site.

These results again indicate that visual landmarks play an important role in accurate orientation along the trunk trails. The next experiments were designed to test the interaction of chemical cues with visual markers.

We selected a well established track of a *P. rugosus* nest. In penetrating a field of snake weed (*Gutierrezia lucida*) the track made two turns, each describing an angle of about 90° (Fig. 22). We removed the snake weed bushes in area B and cut a new track through the field (A); thus

**Table 4.** The distribution of recaptured marked ants (*P. rugosus*) on three trunk trails (see Fig. 21-I). a (yellow): ants which were marked on track A; c (blue): ants which were marked on track C. For further explanation see text

Day	Track A		Track B		Track C	
	a (yellow)	c (blue)	a (yellow)	c (blue)	a (yellow)	c (blue)
8.VII.73	47	0	0	0	0	19
9.VII.73	29	0	0	0	0	29
10.VII.73	8	0	2	1	2	52
11.VII.73	25	0	0	0	1	17
12.VII.73	12	0	3	1	3	10
14.VII.73	19	0	0	0	4	14
16.VII.73	17	4	2	3	0	22
18.VII.73	9	1	7	0	0	30
Total	166	5	14	4	10	193

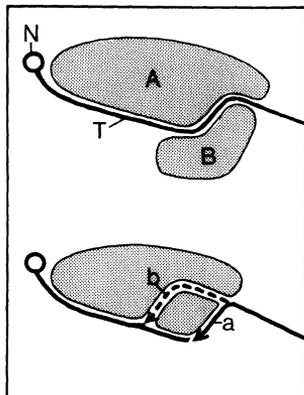
**Table 5.** The distribution of captured marked ants (*P. rugosus*) on three trunk trails (see Fig. 21-II). a (yellow): ants which were marked on track A; c (blue): ants which were marked on track C

Day	Track A		Track B		Track C	
	a (yellow)	c (blue)	a (yellow)	c (blue)	a (yellow)	c (blue)
28.VII.74	21	0	0	7	0	12
30.VII.74	43	0	0	1	0	10
2.VIII.74	32	0	0	12	0	24
4.VIII.74	14	0	0	9	0	16
Total	110	0	0	29	0	62

**Table 6.** Distribution of recaptured marked ants on four trunk trails of a *P. rugosus* nest (see Fig. 21-III), before and after a rich food source was offered at track D

	Track A	Track B	Track C	Track D
Before seeds were offered at D	39.3 ± 24.5	2.2 ± 3.0	0.7 ± 0.8	0.3 ± 0.6
After seeds were offered at D	13.7 ± 6.8	0.5 ± 0.7	0.6 ± 0.8	7.2 ± 3.7

the 90° turns were displaced for about 75 cm. Then we compared the frequently of ants homing along the old track (a) to that of the new track (b). These manipulations caused a considerable disturbance and the total number of homing ants during the next 5-minute period decreased from 233 to 121 ants, 78 of which followed the old track (a) and 43 of which chose the new track. Since the new track had a "visual image" resembling that of the former track, we can assume that a considerable number of ants (43) was guided by the visual markers alone. However, since the "visual image" of the old track was completely changed, those ants (78) which still followed



**Fig. 22.** *P. rugosus* nest (*N*) with a trunk trail (*T*). The track penetrates a snake weed field (*A*, *B*). Below: during experimentation part *B* of the field was removed and a new track (*b*) was cut through the field *A*. For further explanation see text

the old route must have been guided by some other cues. That these are most likely chemical cues can be concluded from the results of the following experiment. When we covered both tracks with a layer of sand, 106 ants followed the new track, apparently now completely dependent on the visual markers, whereas only 26 chose the old route.

Similar experiments conducted with *P. rugosus* and *P. barbatus*, where artificial and natural landmarks along the trunk trails were manipulated, clearly demonstrated that both visual markers and chemical orientation cues are responsible for a precise trunk trail orientation (see also Fig. 20).

Although *P. barbatus* and *P. rugosus* orient along their trunk trails precisely even under completely overcast skies, displacement experiments showed that orientation in respect to the azimuth of the sun also plays an important role. In fact, sun orientation may be the most dominant cue in guiding foragers through terrain poor in topographical structure (Hölldobler, 1971).

In summary, we can conclude that the precise orientation along the trunk trails is achieved by astromenotaxis, as well as by reference to chemical and visual signposts.

As already mentioned, most foragers leave the trunk trails and disperse on individual foraging excursions. The distances of the individual explorations vary greatly, from less than one meter to more than 15 meters. But when homing, the foragers return to the trunk trail very accurately. We marked and followed the individual tracks of 160 *P. barbatus* and 110 *P. rugosus* workers. Almost 86% (239) of the individuals of both species returned to their trunk trails almost at the spot where they had left it (no deviation larger than 100 cm). In several experiments we were able to demonstrate that visual landmarks are used at least in part by the individual foragers to orient back to the trunk trail. This will be illustrated by the following example. The end of the trunk trail of a *P. barbatus* nest was marked by two conspicuous bushes. To get a quantitative measure for the precision of orientation we recorded the time individual homing foragers needed to return to the trunk trail from a distance of 4 m ( $0.83 \pm 0.26$  min;  $n=40$ ) and compared this time with that needed after the two bushes had been removed ( $1.73 \pm 0.48$  min;  $n=39$ ). The difference is highly significant ( $p < 0.0005$ ). After the bushes had been removed the ants

**Table 7.** Site fidelity of a *P. barbatus* nest and a *P. maricopa* nest (no trunk trails). The environs of the nest were subdivided into 8 sectors. A total of 250 ants were marked in sector IV, and the number of ants recaptured during several observational periods in the next three days was pooled. For further explanation see text

	Sector							
	I	II	III	IV	V	VI	VII	VIII
<i>P. barbatus</i>	0	2	9	22	4	1	0	0
<i>P. maricopa</i>	1	0	5	10	6	2		

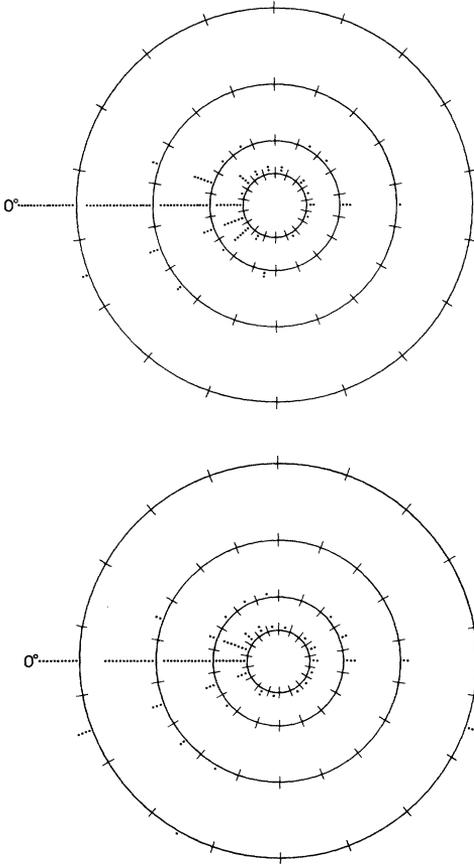
exhibited zigzag runs and conducted searching circles until they reached the trunk trail. Similar results have been obtained on other trunk trails of *P. barbatus* and *P. rugosus*. Thus we can conclude that visual markers play an important role in locating the trunk trail, when the ants return from their individual foraging excursions.

### c) Site Fidelity and Home Range Orientation of Foragers of Nests without a Trunk Trail System

Although most of the *P. barbatus* and *P. rugosus* nests in our study area had extensive trunk trail systems, a number of nests, especially in areas with wider spacing patterns, had no trunk trails. This is a general trait of *P. maricopa*, which we never observed to produce long-lasting trunk trails. In these cases ants usually leave the nest on their individual foraging excursions and frequently disperse in all directions. However, as our experiments demonstrated, foragers in these nests also show a high directional fidelity. We subdivided the foraging area of a *P. barbatus* and a *P. maricopa* nest into 8 sectors and marked 250 foragers in one sector of each nest. During the mornings and afternoons of the following 3 days we counted all marked ants captured in the 8 sectors. As Table 7 shows, by far the most marked ants were found in the sector of close to it where they had been marked.

When foragers of those nests were displaced to the opposite direction while they were still 15 m away from the nest, most of them continued to keep the correct astromenotactic course for 4–8 m before starting to conduct searching circles. It might be supposed that *Pogonomyrmex* can also use a time-compensated orientation to the sun's position or to the pattern of the polarized light of the sky, as it has been previously shown for other ant species (Jander, 1957). In fact, the time-compensated astromenotaxis might be one of the underlying mechanisms for the high directional fidelity of individual foragers. This hypothesis was tested in the following way.

Homing foragers were confined in a dark box at 9:00 a.m. while they were still 20 m from the nest. After 5–8 hrs they were released in a completely unfamiliar flat and sandy area. Around the release point we had drawn eight concentric circles. The smallest had a radius of 2 m, the radius of each of the larger circles was increased by 1 m. The circles were subdivided into 20°



**Fig. 23.** Sun compass orientation of *P. rugosus* and *P. maricopa*. Homing foragers were confined in a dark box at 9 a.m., while they were still 20 m from the nest. After 5–8 hrs they were released in an unfamiliar area. Each point where the ants crossed the circle drawn around the release point was noted. Radius of first circle=2 m; second circle=4 m; third circle=6 m; fifth circle=8 m; 0°=original homing direction; (above: *P. maricopa*, below: *P. rugosus*)

sectors. The marked ant was released in the middle of a seed patch. This is important, because many of the ants only started to show homing orientation after they had picked up a seed. Many of the released ants first stood still for a few seconds, then searched around randomly before taking a seed and running off. Each point where the ants crossed the circles was noted. The 0° direction was always the original homing direction.

As Fig. 23 shows, *P. rugosus* as well as *P. maricopa* workers show a distinct time-compensated astromenotaxis. Similar results were obtained with *P. barbatus*. The few experiments we could conduct when the sun was covered by clouds and patches of blue sky were visible indicated that the pattern of the polarized light also seems to be sufficient for a compass orientation.

The time-compensated astromenotaxis seems to be the major cue for the individual foragers of *P. maricopa*, when they leave the nest. This is probably also true for those workers of *P. barbatus* and *P. rugosus* that do not use a trunk trail system. When we removed horizontal landmarks (bushes) or added additional ones in the foraging area, the directional fidelity of these foragers was not significantly affected. Landmarks are, however, important for orientation on the return run to the nest. This was demonstrated in many experiments. I will report here two typical cases.

**Table 8.** *P. barbatus* workers returning to a nest without a trunk trail were displaced sideways for various distances while still 20 m from the nest. The time the displaced ants needed to find the nest entrance was used as a measure for the accuracy of their orientation. For further explanation see text

Distance of sideways displacement (east) in meters	Percentage of ants needing more than 6 min to reach the nest entrance	Mean time in minutes to reach the nest entrance	Number of ants tested
0	0	$3.9 \pm 0.9$	54
1.5	0	$4.9 \pm 0.6$	30
3	36.3	—	55
6	100	—	58
10	100	—	70

(1) Although one of the *P. barbatus* nests had a long trunk trail leading through thick vegetation to a foraging area 25 m from the nest, many of the foragers dispersed in the opposite direction on individual foraging excursions. They had to run over a sandy, completely cleared area before they reached the foraging ground 27 m away. The location of the nest was distinctly marked by three bushes. If homing foragers, still 20 m away from the nest, were displaced sideways for various distances, they kept their astromenotactic course for 12–16 m, before they made course corrections or started to run in searching circles. The time needed to locate the nest increased considerably with a sideways displacement of more than 2 m (Table 8). Furthermore, the mean time foragers normally needed for homing when still 10 m away from the nest was  $2.1 \pm 0.2$  min ( $n=22$ ). After we had removed the three bushes, the mean time increased to  $3.3 \pm 0.8$  min ( $n=43$ ). Even when close to the nest, homing foragers had considerable difficulty finding the nest entrance. Frequently they ran over the nest and passed the entrance; after travelling 1 to 1.5 m they turned around, conducted searching loops, and finally located the nest entrance.

These results suggest that in the last phase of the return run especially, visual markers play an increasingly important role in locating the nest. The second experimental series, conducted with *P. maricopa*, further supports this hypothesis.

(2) An artificial landmark (dark green cardboard  $75 \times 100$  cm with white patterns, Fig. 24) was placed 1.5 m from the entrance of a *P. maricopa* nest. It remained there for 10 days, after which the orientation experiments were begun. Homing ants starting at 20 m distance needed  $3.8 \pm 0.3$  min ( $n=35$ ) to return to the nest. After the artificial landmark was removed this time increased significantly, to  $5.2 \pm 1.3$  min ( $n=50$ ). In all these cases the homing runs were in a straight line until the ants reached the nest yard, about 4 m from the nest entrance. It was here that the ants started to move in searching loops and circles. Normally homing foragers needed only  $41.8 \pm 7.2$  sec ( $n=15$ ) to move from this point to the nest entrance. After the visual marker had been removed, however, this time increased to  $2.7 \pm 0.8$  min ( $n=36$ ).

This result suggests that the ants' precise orientation was affected by the manipulation of the visual landmarks primarily in the last phase of the homing run. Similar results were obtained with 8 other *P. maricopa* nests. The distances at which the visual landmarks became important varied from ca. 4 m to ca. 8 m, apparently dependent on differences in the topographical structure of the nest environment.

Additional evidence for the significance of a combination of astromenotaxis and topographical orientation during foraging in *P. maricopa* was provided

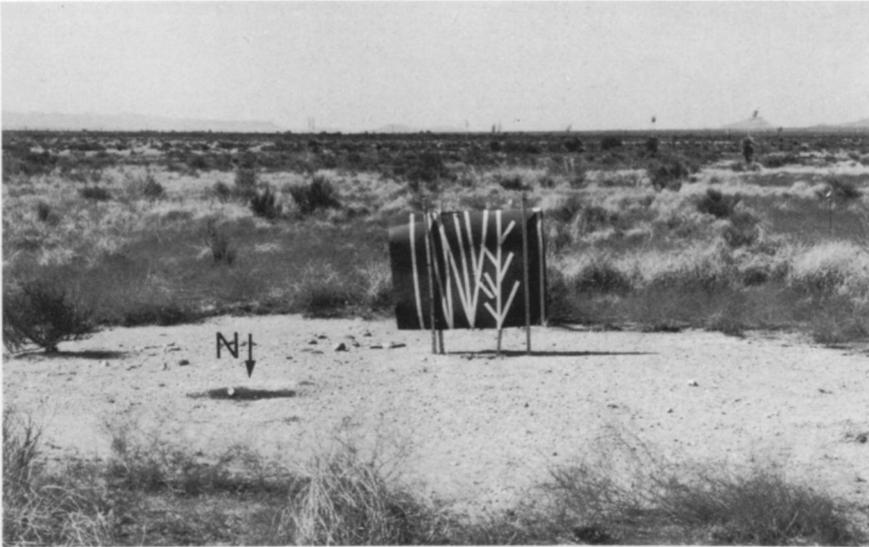


Fig. 24. Artificial landmark set up in the nest yard of a *P. maricopa* nest (N)

by the comparison of the distances of foraging excursions conducted under clear skies to those conducted under complete overcast skies. As Table 9 shows, ants ventured twice as far out of the nest when the sun or blue sky was visible than when the sky was completely overcast. In other words, if *P. maricopa* workers are not able to employ sun compass orientation they do not venture far beyond the familiar topography of the nest area.

#### 6. Agonistic Behavior and Territoriality

A territory is generally defined as an area which the animal or the animal society uses exclusively and defends against intraspecific and sometimes even interspecific intruders (for a comprehensive discussion of the relevant literature see Wilson 1975). Territorial aggressiveness both within and between species has been frequently observed in ants (Wasmann, 1905; Forel, 1921; Elton, 1932; Talbot, 1943; 1954; Way, 1953; Brian, 1955; 1956; Haskins and Haskins, 1965; Pontin, 1961; 1963; 1969; Yasuno, 1965; Hölldobler, 1974; and others; for reviews see Brian, 1965; Wilson, 1971; Carroll and Janzen, 1973). According to these findings three basic types of aggressive encounters can be distinguished: (1) aggression on a colony level, whereby workers of a colony attack workers of another colony nearby; (2) aggression of workers of a colony against colony-founding queens; and (3) aggression between foundress queens. All three types of aggressive interactions were observed in *Pogonomyrmex*. They were found to be the principal mechanisms for overdispersion in these species.

**Table 9.** Foraging distances of individual workers of one *P. maricopa* nest under clear sky (observations during 5 different days) and under completely overcast sky (observations during 3 different days)

Foraging distances in meters under clear sky (sun or at least blue sky is visible)	Foraging distances in meters under heavy overcast sky (neither sun nor blue sky visible)
24.9 ± 7.8 (n=22)	9.9 ± 3.2 (n=18)
22.9 ± 7.6 (n=22)	10.4 ± 3.6 (n=16)
24.8 ± 8.6 (n=16)	11.6 ± 3.4 (n=18)
21.4 ± 4.7 (n=11)	
22.1 ± 4.4 (n=12)	

#### a) Aggression on a Colony Level

The partitioning of space in the field between colonies is effective in reducing aggression between individuals belonging to the same species but to different colonies. As already pointed out, trunk trails used by *P. barbatus* and *P. rugosus* during foraging and homing have the effect of avoiding massive aggressive confrontations between neighboring colonies, while enlarging the foraging area for patchy food supplies. They channel the mass of foragers of hostile neighboring nests into diverging directions before each ant pursues its individual foraging effort. The trunk trails, as well as the immediate surrounding ( $\varnothing$  ca. 2 m) of the nest entrance of mature *P. barbatus* and *P. rugosus* nests can be considered to be the “core area” of the colony’s territory. It is the area of the “heaviest regular use within the home range” (Wilson, 1975) and is absolutely exclusive for members of other conspecific colonies. If, by experimental means, (see p. 23) two trunk trails of neighboring colonies are made to encounter, heavy aggressive mass confrontations occur (Fig. 25). Although foraging areas of nearby colonies often overlap, fighting there is usually limited to individual confrontation between two foragers. However, there is clearly a difference in the fighting intensity at the core area and at the foraging ground, a distinction which is demonstrated by the following data.

In Table 10a the duration of individual aggressive confrontations both within and between the species of *P. barbatus* and *P. rugosus* at the foraging grounds are compared with the duration of fights on the trunk trails (Table 10b). In the first part of the Table I pooled all data obtained during the entire research period. The data in the second part are based on 6 field experiments, during which the trunk trails were made to encounter as described on p. 23. The comparison of both groups of these data clearly demonstrate that fighting inside the core area tends to be much more prolonged than that at the foraging grounds. Furthermore there is no significant difference in intra- and interspecific confrontation in these two species. We can infer from these results that agonistic behavior is considerably more vigorous at the trunk trails and in the nest



**Fig. 25.** Fighting between *P. rugosus* workers belonging to neighboring nests (Photograph: Turid Hölldobler)

yard around the entrance than at the foraging grounds. One additional interesting observation must be mentioned here. In a series of experiments we displaced a number of ants from a trunk trail to near the nest entrance of a nearby conspecific colony. Not surprisingly, fierce fighting almost always ensued. Surprisingly, however, the fighting did not continue for long at the same spot;

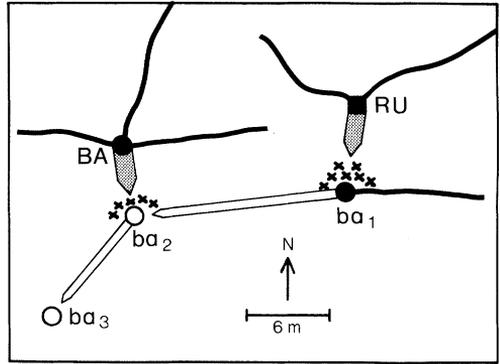
**Table 10**

A. Duration (in seconds) of individual fights both within and between *Pogonomyrmex* species at the foraging grounds. Data are pooled from observations made during the entire research period

	1–30 sec	30–60 sec	> 60 sec	<i>N</i>
<i>P. barbatus</i> / <i>P. barbatus</i>	51.3%	17.3%	31.4%	277
<i>P. rugosus</i> / <i>P. rugosus</i>	45.9%	30.3%	23.8%	462
<i>P. barbatus</i> / <i>P. rugosus</i>	61.0%	23.1%	15.9%	277

B. Duration (in seconds) of individual fights both within and between *Pogonomyrmex* species on the trunk trails. Data are pooled from six experiments (two for each combination) where the trunk trails were experimentally caused to intersect

	1–30 sec	30–60 sec	> 60 sec	<i>N</i>
<i>P. barbatus</i> / <i>P. barbatus</i>	20.5%	6.6%	72.9%	259
<i>P. rugosus</i> / <i>P. rugosus</i>	14.9%	20.1%	65.0%	488
<i>P. barbatus</i> / <i>P. rugosus</i>	27.1%	28.9%	44.4%	387



**Fig. 26.** Schematic illustration of a colony expulsion. The *P. rugosus* colony (*RU*) attacks a *P. barbatus* colony (*ba 1*); *ba 1* emigrates to a new nest site (*ba 2*). There it is attacked by a *P. barbatus* colony (*BA*) and emigrates a second time to *ba 3*. For further explanation see text

instead the displaced ants were rather dragged or even carried by the nest inhabitants 10–18 m away from the nest and then released. The inhabitants quickly returned to their nest, whereas the displaced ants searched around randomly, and only a few were observed to find their way back to their own nest. A similar behavior has been reported in *Manica rubida* (Le Masne, 1965) and *Leptothorax acervorum* (Dobrzanski, 1966). From these experiments we can conclude that the farther away from its nest the intruder is, the less vigorous are the aggressive confrontations with the defenders. Only when neighboring colonies are located too closely together will increased aggressive interactions eventually lead to the emigrations of the weaker colony. In several cases we were able directly to witness such a colony expulsion. I will describe only one particular case, which demonstrates that interspecific aggressive interactions between *P. barbatus* and *P. rugosus* can be as equally effective as intraspecific confrontations.

The situation is depicted in Fig. 26. On 10 July 1974, we observed fighting between *P. barbatus* and *P. rugosus* workers around the *P. barbatus* nest (*ba 1*). After 6 days (16 July) and increasing number of workers from the *P. rugosus* nest (*Ru*) moved toward the *P. barbatus* nest (*ba 1*) which was only 6 m away and fighting intensified. On 17 July we observed the first signs of a colony emigration of *P. barbatus* from *ba 1* to the new nest site *ba 2*, which was 15 m away (Fig. 26). Larvae, pupae and workers were carried to this new nest. During the next four days (17 July–21 July) there was continuous “cross-moving” from *ba 1* to *ba 2* and back from *ba 2* to *ba 1*. Generally, however, the emigration flow toward *ba 2* was stronger. Finally, on 23 July, the whole colony seemed to have moved to its new nest *ba 2*. But ten days later, the colony was on the move again. Some workers moved back to *ba 1*; however, most moved to another new nest site, *ba 3*. Apparently heavy fighting with workers of the neighboring *P. barbatus* colony (*BA*), only 5 m away from *ba 2*, forced colony *ba 2* to emigrate again. It took 6 more days before the colony finally settled in *ba 3*.

This was one of the most impressive cases of colony expulsion we witnessed during the entire course of our field work. The episode lasted more than 30 days. From a total of ten additional colony confrontations, which we observed to lead to the emigration of one of the colonies involved, 5 occurred between *P. barbatus*, 2 between *P. rugosus*, 2 between *P. maricopa*, and one between *P. barbatus* and *P. rugosus*.

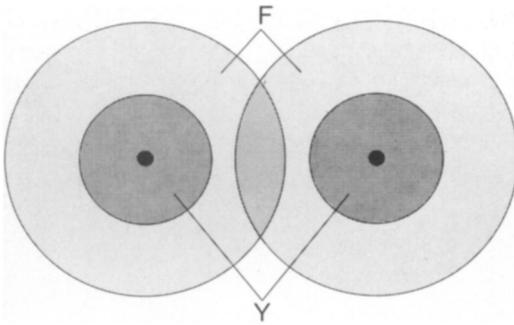


Fig. 27. Schematic illustration of the nest yards and overlapping foraging areas of two neighboring *P. maricopa* colonies. *F* foraging area; *Y* nest yard

Although *P. maricopa* nests usually do not create a trunk trail system, they nevertheless possess an equivalent exclusive “core area.” The core area is the “nest yard” around the nest entrance, which is frequently completely cleared of vegetation and with a diameter of approximately two to ten meters. As Fig. 27 schematically illustrates, the foraging areas of neighboring colonies can overlap. The nest yards, however, are always entirely separated. If individual foragers of different colonies meet in the foraging area, fighting ordinarily ensues. As Table 11 demonstrates, these intraspecific fights within *P. maricopa* are usually longer lasting than interspecific confrontations of *P. maricopa* with *P. barbatus* or *P. rugosus*, respectively (Table 11a). Under normal conditions intraspecific fights are only rarely observed inside the nest yard of a *P. maricopa*

**Table 11**

A. Duration (in seconds) of individual fights both within and between *Pogonomyrmex* species at the foraging grounds. Pooled data are based on observations made during the entire research period

	1–30 sec	30–60 sec	< 60 sec	<i>N</i>
<i>P. maricopa</i> / <i>P. maricopa</i>	43.0%	36.3%	20.7%	242
<i>P. maricopa</i> / <i>P. barbatus</i>	81.6%	11.8%	6.6%	119
<i>P. maricopa</i> / <i>P. rugosus</i>	71.9%	19.3%	8.8%	192

B. Duration (in seconds) of individual fights both within and between *Pogonomyrmex* species in the nest yard of *P. maricopa* nests. The data of the first column are based on observations after workers of a nest were experimentally displaced into a nest yard of a neighboring colony. The pooled data of the other two columns are based on observations made during the entire research period

	1–30 sec	30–60 sec	> 60 sec	<i>N</i>
<i>P. maricopa</i> / <i>P. maricopa</i> (experimentally induced)	11.7%	23.3%	65.0%	60
<i>P. maricopa</i> / <i>P. barbatus</i>	70.9%	20.9%	8.2%	182
<i>P. maricopa</i> / <i>P. rugosus</i>	85.3%	12.7%	2.0%	300

colony, whereas interspecific encounters with *P. barbatus* or *P. rugosus*, respectively, occur quite frequently. In the latter cases fights are usually of very short duration (Table 11 B). When we displaced workers of a *P. maricopa* nest into the nest yard of a conspecific neighboring nest, intensive fighting resulted and the individual aggressive actions lasted much longer than interspecific fights induced by a similar procedure. In many cases involving *P. maricopa* the foreign intruders were dragged or carried away from the nest yard and were dropped often more than 15 m away from the nest entrance.

#### b) Exclusion of Founding Queens from the Nest Territory

The phenomenon of aggression by workers of mature colonies against founding queens and young colonies has been well documented in several ant species (Brian, 1955, 1956, 1965; Pontin, 1960; Marikovsky, 1962; and others; see reviews in Wilson, 1971; Carroll and Janzen, 1973). Our quantitative study on queen expulsion from the nest territories of mature *Pogonomyrmex* colonies support Brian's conjecture that aggression against founding queens is one of the major mechanisms bringing about spacing within species.

After the nuptial flights, which occur in July and August, thousands of queens wander around searching for a suitable place to dig their founding chambers. It is also during this time that workers of mature colonies literally pour out of the nest entrance and disperse in all directions while exhibiting highly aggressive behavior. Fighting intensity between workers of mature neighboring colonies is considerably increased. If young queens venture too close to a nest of their own species, they are in most cases soon discovered and fiercely attacked. However, on the many occasions we observed these interactions, only seldom were the queens injured or killed. In most cases they were dragged or even carried 10–15 m away from the nest and dropped. After we observed this exclusion behavior repeatedly, we undertook a more quantitative study by releasing young queens 30 cm from the nest entrance of mature colonies. All these experiments were conducted after a nuptial flight period in the late afternoon. Table 12 shows the results of a series of experiments during which we released *P. barbatus* queens at four different *P. barbatus* nests. As can be seen the data vary considerably; however, it is obvious that most of the queens are dragged to the territorial border (mean 49.6%; range 24.0–68.5%). Furthermore, a considerable number of queens escaped without being seriously attacked at all (mean 38.0%; range 25.8–47.5%), so that the number of queens which were injured (mean 12.4%; range 0–34%) were the smallest group. Similar results were obtained with *P. rugosus* and *P. maricopa* (Table 12). We also released *P. barbatus* queens at nests of *P. rugosus*. Table 12 shows also that these responses of the defending workers do not differ significantly from those seen in the intraspecific tests. Unfortunately we did not have enough *P. maricopa* queens to test the interspecific response toward these females. The few data we obtained indicate that *P. maricopa* queens are fiercely attacked by their own species but more easily escape attacks by *P. barbatus* and *P. rugosus*.

**Table 12.** Young *Pogonomyrmex* queens were released at mature nests. For further explanation see text

Nest	Queens injured (%)	Queens carried or dragged (%)	Range of distances queens carried or dragged (meters)	Mean distances queens carried or dragged (meters)	Queens escaped (%)	Total number queens tested
A. <i>P. barbatus</i> at <i>P. barbatus</i> nests						
I	10.0	53.3	1.5–21	18.1 ± 10.0	36.7	60
II	5.7	68.5	3–17	12.0 ± 6.7	25.8	35
III	0	52.5	7–15	11.7 ± 6.4	47.5	40
IV	34.0	24.0	8–19	13.2 ± 3.5	42.0	50
B. <i>P. maricopa</i> at <i>P. maricopa</i> nests						
I	2.2	13.3	8–25	17.0 ± 6.9	84.5	45
II	0	0	—	—	100.0	20
III	8.6	5.7	17–18	—	85.7	35
IV	15.0	17.5	14–21	18.0 ± 2.3	67.5	40
C. <i>P. rugosus</i> at <i>P. rugosus</i> nests						
I	20.0	80.0	4–14	10.2 ± 2.9	0	20
II	0	36.7	6–17	12.1 ± 3.6	63.3	30
D. <i>P. barbatus</i> at <i>P. rugosus</i> nests						
I	21.8	23.6	6–16	11.6 ± 3.2	54.6	55
II	17.5	12.5	8–14	11.2 ± 2.6	70.0	40

Despite the fact that many queens are driven away before they can begin digging a nest chamber, some do succeed in settling near a mature colony. Freshly built incipient nests can be recognized by the ring of excavated soil around the closed nest entrance. After each nuptial flight we searched the surrounding area of several mature *Pogonomyrmex* nests up to a distance of 9 m from the nest entrance, and excavated each founding chamber. In Table 13 all data gathered from the survey of a total of 72 *P. barbatus* nests have been pooled. We found 58 founding chambers of *P. barbatus*, 28 of *P. rugosus* and 97 of *P. maricopa*.

However, even if a founding queen succeeds in building her nest chamber near a mature colony of the same species, she is not yet safe. As reported from some other ant species, workers of mature *Pogonomyrmex* colonies frequently discover the founding nests and turn the queens out. It is interesting to compare the data shown in Table 13 with the number of nest excavations conducted by *P. barbatus* workers actually observed. Of a total of 44 excavations, 30 were directed against *P. barbatus* queens, 10 against *P. rugosus* queens and only 4 against *P. maricopa* queens, although the latter species was the most abundant one found in our survey (Table 13). From this we may conclude that *P. barbatus* workers can discriminate between nest chambers of queens of their own species from those of *P. maricopa*. Since generally fewer *P. rugosus*

**Table 13.** Number of young *Pogonomyrmex* queens found which had excavated incipient nests near mature colonies of *P. barbatus*. Data are based on the survey of a total of 72 nests

Distance from the nest entrances of <i>P. barbatus</i> colonies (meters)	Number <i>P. barbatus</i> queens	Number <i>P. rugosus</i> queens	Number <i>P. maricopa</i> queens
1-2	0	0	0
2-3	3	4	4
3-5	11	5	16
5-7	15	12	28
7-9	29	7	49
Total	58	28	97

queens are found around *P. barbatus* nests (Table 13), obviously due to differences in the overall distribution of the populations of both species, a discrimination between *P. barbatus* and *P. rugosus* queens cannot be inferred from our data. Furthermore, nest chambers of queens of *P. barbatus* and *P. rugosus* were found close to *P. maricopa* nests, but only on two occasions did we observe *P. maricopa* workers excavating a *P. barbatus* female and only once a *P. rugosus* queen. On the other hand, we observed a total of 7 excavations of *P. maricopa* queens by *P. maricopa* workers. These observations further support our thesis of intra- and interspecific discrimination. These field observations are being currently tested in laboratory experiments which are designed to analyze the behavioral mechanisms of species discrimination.

Finally it must be mentioned that the sympatric species *Novomessor cockerelli* also plays an important role in controlling the number of founding queens of *Pogonomyrmex*. We witnessed 8 queens of *P. barbatus*, 3 of *P. rugosus* and 5 of *P. maricopa* being excavated by *Novomessor* workers. In these cases the queens were killed and brought to the *Novomessor* nest as prey. Furthermore, *Novomessor* frequently acts as a predator at the mating leks of *Pogonomyrmex* (Hölldobler, unpubl.) preying on alate males and females.

### c) Territoriality between Foundress Queens

Frequently colony-founding ant queens and juvenile colonies are more abundant where mature colonies are scarce or absent. Brian (1955, 1956a, b), who has studied this effect in the British fauna in some detail, discovered a striking inverse correlation in various habitats between the density of adult colonies and of foundress queens of *Formica* and *Myrmica*. *Pogonomyrmex* is no exception; in some areas, where there is relatively little interference from mature colonies, the density of foundress nests is markedly higher. Sometimes nest chambers are as little as 5 cm apart. But even on the "foundress queen level"

there exists already a strong territoriality. In the course of excavating hundreds of founding queens of *P. barbatus*, *P. maricopa* and *P. rugosus*, not once did we find two or more queens together in one chamber. Obviously, *Pogonomyrmex* queens found their colonies under natural conditions strictly in solitude, and possibly never in pleometrosis (alliance). On one occasion I was able to observe a searching *P. barbatus* female enter the hole of another queen's chamber. Within seconds the resident pulled the intruder out of the nest and dragged her ca. 3 m away. After she had dropped the foreign female she quickly returned to her nest. Inspired by this observation I induced similar situations 15 times, by placing searching females close to the nest entrance of another queen. Searching females often readily accept preformed little holes to begin building their nest. All introduced queens were marked with a yellow spot. Eight times the response of the "owner queen" was similar to that described above: not much time was wasted with fighting; the intruder was simply dragged or carried up to 4 m away from the nest. In seven other cases the intruder was instantly repulsed and departed. These observations were further confirmed by the following series of laboratory experiments.

Females of *P. barbatus*, *P. maricopa* and *P. rugosus* collected after a nuptial flight and kept together in containers exhibit almost no aggressive behavior. On the contrary they usually aggregate. However, as soon as they occupy their own nest chamber, an impressive territorial behavior is manifested. Of 100 *P. barbatus* queens collected at the same time, 50 were kept in a plastic box (30 × 30 cm), the bottom of which consisted of moist gypsum and a 2 cm thick layer of sand (Box I). The remaining 50 females were placed in a similar box (Box II) which had an 8 cm thick layer of moist sand into which 36 holes ( $\varnothing=0.7$  cm) punched each 5 cm deep. The holes were regularly spaced, 5 cm apart. During the next 3 weeks both boxes were regularly observed. In Box I we noted only 4 short fights; in Box II, however, 27 fights were observed and 58 times queens were seen dragging another queen out of a hole. Similar results were obtained with *P. rugosus* and *P. maricopa*. These experiments have been repeated several times, always producing essentially the same results. They are being currently continued in order to analyze the behavioral mechanisms of territoriality and dominance in foundress queens of *Pogonomyrmex*.

## Discussion

Since individual harvesting ants (*Pogonomyrmex*) usually collect scattered seeds, casual observations in the past have seemed to indicate a foraging system based on individual initiative and orientation. But in the experiments described here and elsewhere (Hölldobler and Wilson, 1970; Hölldobler, 1971) we have proved that *Pogonomyrmex* uses recruitment pheromones released from the poison gland. Working with the three sympatric species *Pogonomyrmex barbatus*, *P. rugosus* and *P. maricopa* in the mesquite-acacia desert in Arizona-New Mexico, we found that all three species recruit nestmates to newly discovered rich food sources. The results reported in this paper have demonstrated that there is no significant difference in the behavioral recruitment patterns of colonies tested in the laboratory and those tested in the field, as suggested by Carroll and Janzen (1973). As revealed by our experiments the recruitment activity depends on a number of parameters of the food source, such as distance to the nest, density of the seed fall, size of the seed patches and size of the grains. Furthermore it is also affected by the presence, absence or distance of hostile intra- and interspecific neighboring colonies.

Since *P. maricopa* generally recruits less efficiently to food sources than do *P. barbatus* and *P. rugosus*, it is interesting to compare briefly the trunk trail foraging strategy typical of *P. barbatus* and *P. rugosus* nests with the more individualistic foraging behavior of *P. maricopa*. The use of chemically and visually marked trunk trails not only guarantees an efficient partitioning of foraging grounds in densely populated habitats; it also allows precise home range orientation and foraging excursions under completely overcast skies, in dense vegetation, and even during the night. Indeed, in parts of southern Arizona (Organ Pipe National Park), we observed that *P. rugosus* shows a nocturnal foraging activity during the hottest part of the summer. We found that the nocturnal foragers depend heavily on their trunk trails for precise home range orientation. Also, *P. barbatus* in southern Texas seems to forage primarily during the night (Box, 1960), whereas in our study area all three *Pogonomyrmex* species ceased foraging at dusk. Although *P. maricopa* occasionally uses short lived chemical recruitment trails to attract nestmates to rich food sources, our experiments revealed that individual ants are guided principally by visual cues. This foraging and orientation strategy obviously does not allow as subtle a partitioning of foraging grounds as the trunk trail strategy. This explains why *P. maricopa* colonies are much more widely spaced (mean distance 46 m) than those of *P. barbatus* (18 m) or *P. rugosus* (19 m) (Table 3).

The different foraging strategies suggest that food used preferentially by *P. barbatus* and *P. rugosus* might have a more patchy distribution than that used by *P. maricopa*. Indeed, our foraging and recruitment experiments show that *P. barbatus* and *P. rugosus* react much more efficiently to a patchy food distribution than does *P. maricopa*. Furthermore, our feeding experiments suggest that *P. barbatus* and *P. rugosus* have a wider breadth of diet in respect to the size of seeds than is the case for *P. maricopa*. If a future quantitative analysis of the food preferences of these three sympatric *Pogonomyrmex* species confirms our suspicions, then the adaptive significance of a wider spacing pattern of *P. maricopa* populations will be clear.

Some sympatric harvester ant species which are apparently identical with regard to food type and nesting site, were found to differ in the time of their daily foraging activity (Bernstein, 1973). This is not the case with the three *Pogonomyrmex* species studied here. Since *P. barbatus* and *P. rugosus* in particular have a wide niche overlap, it is not surprising that territoriality is strongly developed both within and between these two species. *P. maricopa*, on the other hand, seems to be more specialized in regard to food, and it is consistent to find that interspecific territoriality with *P. barbatus* and *P. rugosus* is less developed. In fact, it is common for *P. maricopa* workers to forage directly around the nests of *P. barbatus* or *P. rugosus*; similarly, foragers of the latter two species can often be observed in the nest yards of *P. maricopa* colonies. In general, aggressive interactions between foragers of *P. maricopa* and *P. barbatus* or *P. rugosus*, respectively, are considerably less intense than those between workers of neighboring *P. maricopa* nests. On the other hand aggression is equally strong both between and within the species *P. barbatus* and *P. rugosus*. Nevertheless, foraging territories frequently overlap and aggressive interactions there are usually less intense than at the core areas (trunk trails plus nest

yards), which normally do not overlap and are vigorously defended. Aggressive confrontations at the colony level and the aggressive expulsion of foundress queens from the nest territories of mature colonies are the main behavioral mechanisms which maintain overdispersion in *Pogonomyrmex*.

These findings lead to the more purely physiological question: What are the cues for recognition and discrimination between species and intra-specific colonies? We have started to search for specific volatile compounds in *Pogonomyrmex* species that may function as species recognition cues (Regnier *et al.*, 1973). We already have evidence of species specificity in the mixture of compounds of the Dufour's glands and are preparing to investigate the possibility of odor discrimination by means of these substances. In addition, Hangartner *et al.* (1970) have shown that *P. badius* workers are able to distinguish the odor of their own nest material from that of other nests. In the course of more recent laboratory experiments we found that even in the trunk trails there exists colony specific chemical cues which enable the ants to choose the trails leading to their own nest as opposed to those leading to a neighboring colony (Hölldobler and Regnier, unpubl.).

However, field experiments have revealed that visual markers play an equally important role to chemical cues in home range orientation and recognition of territorial borders. Individual groups of foragers become intimately familiar with particular sections of the foraging area. This spatial foraging specialization enables the colony as a whole to extend its foraging range considerably. This is especially true for those nests that employ a trunk trails foraging strategy, as many *P. barbatus* and *P. rugosus* colonies do. The colony's foraging field consists of a "large patchwork of intensively visited areas," mingled with other large areas that are less frequently visited but may be extensively used by the forager force of a neighboring colony. New foraging sites are rapidly explored and occupied with the aid of an effective chemical recruitment system. The significance of the recruitment communication becomes especially apparent in view of the strong intra- and interspecific competition for the same foraging areas.

A similar foraging system has been reported in many *Formica* species (Dobrzanska, 1958; De Bruyn and Mabellis, 1972; Horstmann, 1972; and others). Rosengren (1971) has recently demonstrated that the remarkable route fidelity of foragers in these species is due to a detailed memory for specific visual cues along the trunk trails. On the other hand, in *P. maricopa*, which has extended nest yards instead of trunk trails, foragers appear to orient by visual cues inside the nest yard but depend largely on sun compass orientation outside. This mode of home range orientation is similar to that described by Wehner and Menzel (1969) for *Cataglyphis bicolor* in Israel. Close to the nest individual foragers orient to visual patterns, whereas farther away they depend completely on astromenotactic orientation. *Cataglyphis* apparently does not employ chemical recruitment or orientation cues. Foragers leave the nest on their individual hunting expeditions. *P. maricopa* hunts in a similar manner, dispersing in all directions. Occasional recruitment trails directed to rich food sources normally do not become established as long lasting trunk trails as is the case in *P. barbatus* and *P. rugosus*.

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