# Ecology of the Ant *Pogonomyrmex mayri*: Foraging and Competition[1]

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## ABSTRACT

Aspects of recruitment and foraging behavior of *Pogonomyrmex mayri* (Myrmicinae: Formicidae) are described. Foragers leave and return to the nest in all directions, but each worker tends to forage only in one sector of the territory. When food is discovered, nestmates are recruited by a trail pheromone, but even with a persistent food source, a single file of foragers never develops. Foragers rarely cooperate to transport prey. Foraging is strictly diurnal with the amount of activity controlled by temperature, which in turn is affected by season, time of day, and nest location. Strong territorial defense by neighboring colonies and competition from other ant species often severely restrict foraging direction and distance.

VIRTUALLY NOTHING IS KNOWN OF THE SOUTH AMERICAN species of the genus *Pogonomyrmex*. The North American *Pogonomyrmex* of the subgenus *Pogonomyrmex* are well known for living in open habitats and collecting and storing large quantities of seeds in underground granaries, and for stinging fiercely when disturbed (Wheeler 1910). It is not known to what degree the subgenera *Ephebomyrmex* and *Forelomyrmex,* which dwell primarily in South America, share those characteristics.

*Pogonomyrmex* (*Forelomyrmex*) *mayri* is a large, velvety black ant whose entire known distribution lies at the foot of the Sierra Nevada de Santa Marta in northeastern Colombia. Kugler (1978) and Kugler and Hincapié (1983) have shown that this species differs morphologically and ecologically from its better-known relatives. Instead of forming large colonies in open desert or grassland, it forms rather small colonies usually at the bases of trees and shrubs in dry forest. It scavenges dry arthropod remains and miscellaneous plant parts by foraging on the soil or leaf litter surface. It does not sting or store seeds. This report makes further comparisons of diurnal activity, territoriality, and recruitment.

## MATERIALS AND METHODS

Most observations come from a study area 33 × 40 m in the forest behind Gairaca Bay of Tayrona National Park, 8 km east of Santa Marta, Colombia. A description of the study site and the means used to locate, mark, and map nests are found in Kugler and Hincapié (1983).

To record the temporal patterns of foraging activity in wet and dry seasons and in the presence and absence of competing ants, I used what will be referred to henceforth as "foraging plots." These plots were 1 × 2 m rectangles outlined by string held several centimeters off the ground by small wire stakes at the corners. They were placed within a meter of a *P. mayri* nest entrance, and each hour the numbers of *P. mayri* and its most likely competitors, *Odontomachus bauri* and *Ectatomma ruidum,* were recorded using the following procedure. First, I placed two mercury thermometers on the ground near the plot, one in shade and one in full sun, and stood immobile at the edge of the plot for five minutes, during which time I estimated the percentage of the plot in direct sun. Then, each species was counted in a separate inspection of the plot, and the thermometer temperatures were recorded. Those temperatures are of course only approximations of the temperatures of the ants. A record of activity throughout the day was obtained by repeating this procedure each hour beginning and ending in darkness. I accumulated 21 such records of diurnal activity using 10 nests in a variety of microhabitats and spanning both wet and dry seasons (November and March, respectively).

Intraspecific competition in foraging was inferred from three types of evidence: (1) mapping the limits of the foraging territories by offering peanut chips to foragers and following them to their nests, (2) luring marked foragers from one colony to the territory of another colony and observing the resulting interactions, and (3) measuring territorial expansion after excavation of a neighboring nest. Mapping was accurate to within 50 cm (Kugler and Hincapié 1983).

Interspecific competition was also studied by removal experiments. Twice I tested whether *P. mayri* limits the foraging of *E. ruidum.* In each experiment, I recorded hourly the numbers of both ants in a foraging plot located 1 m from a *P. mayri* entrance. Then the foragers of that colony were removed by entrapment in the nest or by excavation, and the hourly activity of *E. ruidum* alone was recorded. In a third experiment, I tested whether *E. ruidum* restricts the foraging of *P. mayri.* The foraging territory of a *P. mayri* nest was mapped and the positions of all *E. ruidum* entrances in and around that territory were marked with small flags. The normal levels of for-

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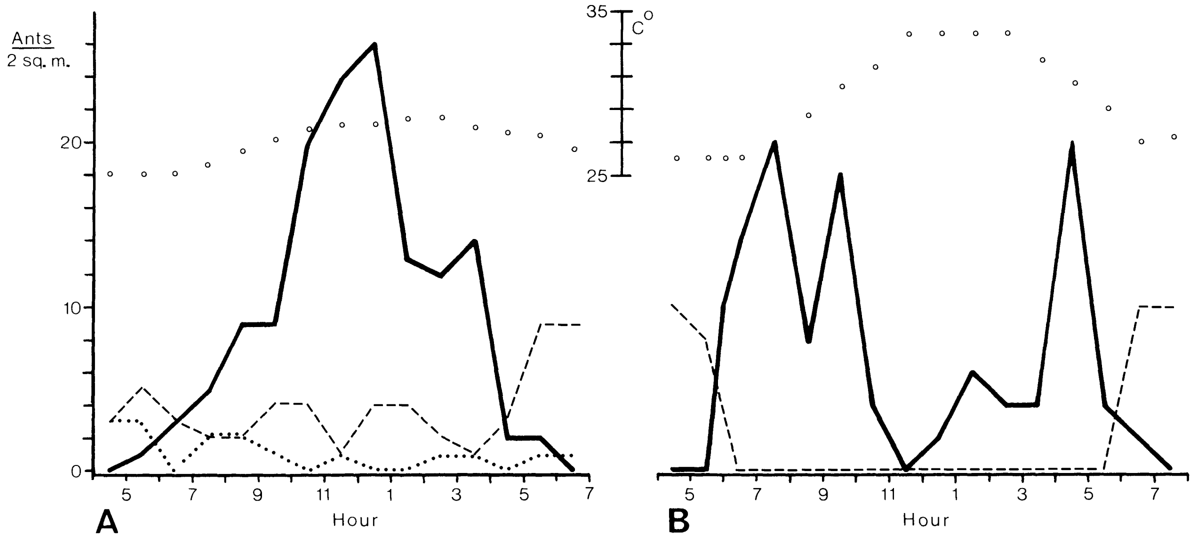

FIGURE 1. Typical diurnal activity of *Pogonomyrmex mayri* in the rainy season (A) and the dry season (B). Each graph is the number of *P. mayri* (solid line), *Ectatomma ruidum* (dashed line) and *Odontomachus bauri* (dotted line) in a 1 × 2 m plot near a *P. mayri* nest, taken at hourly intervals. Ground temperature in the shade (unconnected circles) is on a separate scale.

aging activity of the two ants were recorded for three days by using two foraging plots, one inside the *P. mayri* territory and one outside it. At 0400 one morning, about two hours before the *P. mayri* would begin to emerge, all marked entrances of *E. ruidum* were plugged. For the next hour, each entrance was visited repeatedly to aspirate any returning foragers, so that by the time *P. mayri* began foraging, the *E. ruidum* population in the area was reduced to nearly zero. The dimensions of the *P. mayri* territory and the numbers of workers in the two plots were recorded for the rest of that day and then again five days later. During the first day, all *E. ruidum* that appeared in the area were removed as soon as possible.

Use of a trail pheromone was demonstrated with the following test repeated 25 times using 10 different nests. A forager about 1 m from its nest entrance was offered a peanut fragment. As it manipulated the bait, it was dabbed with white fingernail polish on its trunk dorsum. Its route to the nest was marked with a row of small twigs placed about 1 cm to the side. If the first unmarked worker that emerged from the entrance followed the recruiter's entire path, a positive trail-following response was recorded. The return path of the recruiter also was noted. Since it was possible that the recruits were following the twigs, in each of three additional tests a row of twigs was set so that it diverged about 15° from the recruiter's path, beginning at the nest entrance. The actual path of the recruiter was mentally noted.

The duration of the trail pheromone was measured using a similar method. A forager was baited and marked and its path paralleled with twigs; then I recorded the number of the recruits that traversed the entire trail each minute from the time the recruiter entered the nest. Both recruits and the recruiter were aspirated as they arrived at the bait site. This test was repeated 25 times with ants from 12 nests.

In a single test, recruitment rate to a long-term food supply was observed by placing piles of peanut chips at 1 m and 4 m from a nest and recording the arrivals in 5-min intervals.

To determine foraging constancy, I marked all workers over the course of several hours that arrived at the far end of one sector. Then in subsequent days, the positions of every marked and unmarked ant in the entire territory were periodically recorded. Three territories were studied in this way.

## RESULTS

Diurnal activity.—*P. mayri* is strictly diurnal in both wet and dry seasons. During March and November, when most of these observations were made, the first foragers emerged at about 0530 and the last returned at about 1830—the approximate times of sunrise and sunset at this 11°N latitude site. Figure 1 shows examples of diurnal activity during the dry and rainy seasons near nests that experienced little interference from competing ants and were shaded only by the canopy.

In March and April during the dry season (Fig. 1B), the naked canopy provided little shade from a cloudless

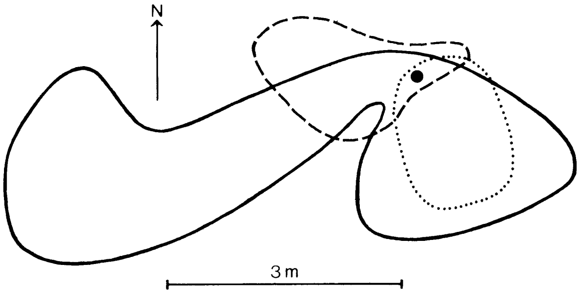

FIGURE 2. The change in foraging area of a *P. mayri* colony during the dry season in response to insolation. The nest entrance (large dot) is at the base of a shrub, and the perimeter of the foraging area is shown at the times of 0600 (dotted line), 0800 (solid line), and 1000 (dashed line). The foragers emerged at about 0530 and foraged at increasing distances from the entrance until the exposed terrain became too hot.

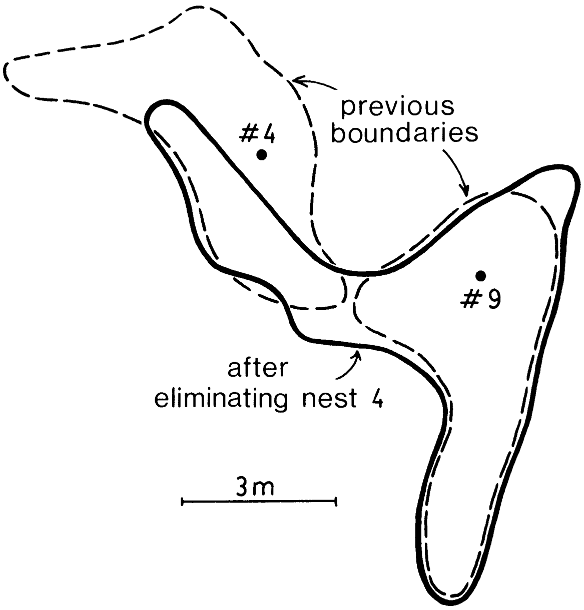

FIGURE 4. The effect of removing one of two neighboring *P. mayri* colonies. Dots represent the entrances of two adjacent *P. mayri* nests. The dashed lines are the maximum territorial perimeters for several days prior to excavation of nest 4; the solid line is the territorial perimeter of nest 9 four days after nest 4 was removed.

sky, and so from 0830 to 1630 30–95 percent of the plot was in direct sun. An hour before and after these times the sun was hidden behind mountain ridges to the east and west. Temperatures in the sun peaked at 53°C (127°F) between 1230 and 1330, during which time the ants retired underground. But during the dry season most colonies located their entrances at the bases of trees or shrubs, so at least their entrances were shaded. This permitted some degree of foraging throughout the day, but foraging areas often had to contract or shift to follow the changing patterns of shade (Fig. 2). In most of these colonies there was marked decrease in foraging activity at midday, but colonies that were particularly well shaded by dense shrubs and vines suffered little or no decline.

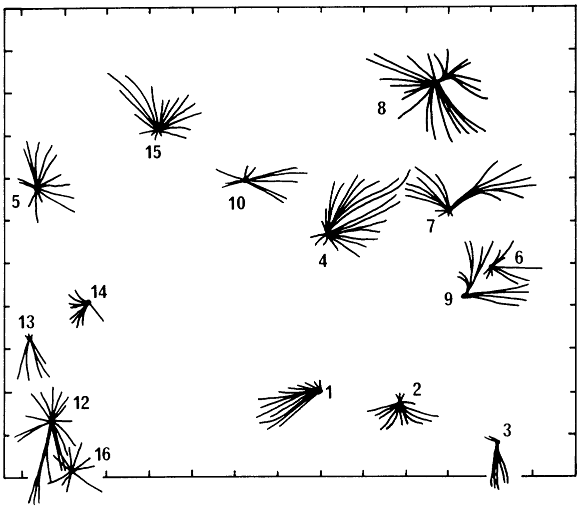

FIGURE 3. Territories of *P. mayri* colonies in the Gairaca study site on one day during the rainy season. Each line represents the path of a forager returning to its nest with bait. Mapping was repeated at different hours and days. One unit on each axis is 3 m.

In November, during the rainy season (Fig. 1A), there was much more haze or cloud cover during the day, and the foliage on the trees and shrubs provided more shade. Even at midday only 5–10 percent of a foraging plot was exposed to direct sun. Ground temperatures were much lower than in comparable dry-season plots: less than 31°C in the sun at midday. In the rainy season *P. mayri* foraging was unimodal with greatest activity at midday, and I did not observe shifting territorial boundaries.

INTRASPECIFIC COMPETITION.—Mapping of nests suggested the presence of foraging territories defended by monodomous colonies (Fig. 3). Although the positions of the nests changed frequently (Kugler and Hincapié 1983), foraging areas of adjacent nests usually were separated by a "no ant's land" about 0.5–1.0 m in width. If overlap did occur, such as between nests 12 and 16 in Figure 3, it was temporary and marked by fighting in the region of overlap.

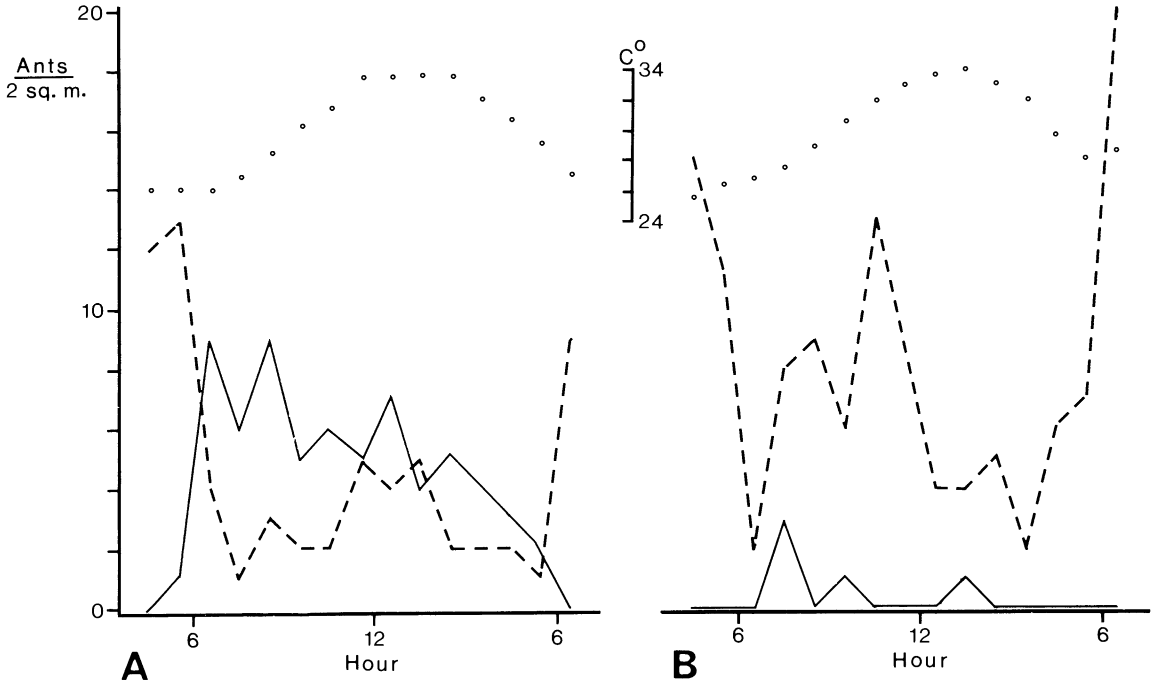

FIGURE 5. The effect of competition from *P. mayri* (solid line) on the foraging of *E. ruidum* (dashed line). A. Numbers of the two species in a 1 × 2 m plot at a distance of 1 m from a *P. mayri* nest before confining the *P. mayri* to their nest. B. Numbers of the two species in the same plot on the second day after removal of *P. mayri* (workers of *P. mayri* removed after each count). Shaded ground temperature, on a different scale, is shown by unconnected dots.

Intercolony aggression and territorial defense were further demonstrated experimentally. Whenever ants from adjacent colonies were simultaneously lured with bait into their no ant's land, they behaved aggressively. On one such occasion, in which the members of one colony were identified with a dab of white fingernail polish, I witnessed 36 interactions between members of the two colonies in the course of a half hour. Only 4 (12.5%) involved neither fight nor flight, 7 (22%) consisted of mutual flight upon detection, 13 (41%) involved flight with chase, and 12 (37.5%) involved aggressive physical contact, from brief pulling on antennae or legs to prolonged balling up with flexing of the gaster. This aggression was not a reaction to the fingernail polish, because previous studies had shown that members of the same colony never displayed any hostility toward their marked nestmates. In this case no encounters ended in harm to either antagonist, but in other border fights some ants were killed.

A removal experiment (Fig. 4) showed the extent to which colonies of *P. mayri* limit the foraging of their neighbors. Before excavating nest 4, workers of nest 9 were rarely seen within a meter of foragers from nest 4, even though no physical barrier intervened. Four days after the removal of nest 4, much of its former territory was occupied by foragers from nest 9. The new boundaries of colony 9 were the same when checked a week later.

INTERSPECIFIC COMPETITION.—The only ant that was observed to interact with *P. mayri* daily and throughout the year was *Ectatomma ruidum,* a ponerine ant the same size as *P. mayri* that also forages diurnally in large numbers on the ground for termites, arthropod remains, and sweet plant parts. Unlike *P. mayri,* though, *E. ruidum* also forages in trees and shrubs, tends honeydew-secreting insects, and is even more active by night than by day. Despite their differences, the two species have considerable niche overlap, and overt aggression was observed between them whenever a large amount of peanut or sweet bait was placed on the ground to attract *P. mayri.* The bait would also attract *E. ruidum* in substantial numbers, and frequently pairs would ball up in brief fights, from which both would leave unharmed. Sometimes *E. ruidum* would dominate a bait and exclude *P. mayri,* and at other times the reverse occurred. Despite the overt aggression between these two species, nest entrances of the polydomous *E. ruidum* were common within the territories of *P. mayri,* some within a meter of the *P. mayri* entrance.

To test whether *P. mayri* has any limiting effect on

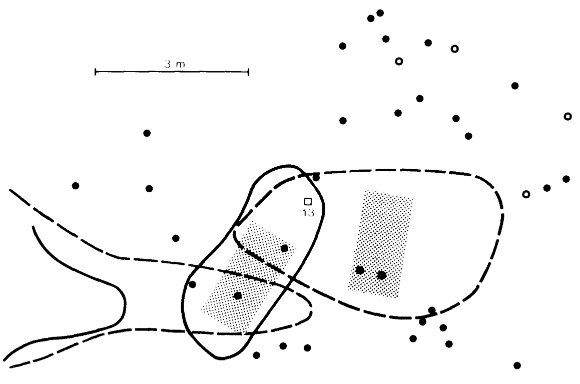

FIGURE 6. The effect of competition from *E. ruidum* on the foraging of *P. mayri*. Territories of two *P. mayri* colonies are shown before (solid lines) and 6 days after (dashed lines) removal of *E. ruidum* from around nest 13. The entrance to nest 13 is represented by an open square. The *E. ruidum* entrances that were found and plugged are shown by solid circles; open circles show entrances not plugged. The shaded rectangles are foraging plots used to monitor activity (see text).

the foraging of *E. ruidum,* I twice set up foraging plots 1 m from *P. mayri* nest entrances and then recorded *E. ruidum* activity before and after removal of the *P. mayri.* Figure 5 shows the results of one experiment. The average number of *E. ruidum* per plot between 0630 and 1730 rose from 19.5 (SD = 13.5) before removal of *P. mayri* to 65.5 (SD = 9.5) after removing nearly all *P. mayri* from the two sites. The increase is significant (*t* test, $P < .01$). So *P. mayri* does seem to reduce *E. ruidum* foraging near its nest entrance, but it is not a strong enough competitor to keep *E. ruidum* from foraging or nesting within its territories.

To test whether *E. ruidum* in turn limits the foraging of *P. mayri,* I observed the effect of removing *E. ruidum* from within and around a *P. mayri* territory. Figure 6 shows two *P. mayri* territories before and after blocking most of the *E. ruidum* entrances around nest 13. It also shows the location of two foraging plots. A plot outside the original territory of nest 13 was in a bare, shaded spot usually preferred by *P. mayri* foragers, yet nest 13 foragers never ventured more than a few centimeters in that direction. Another plot was entirely within the original territory of nest 13. With the removal of *E. ruidum,* the nest 13 territory enlarged to include both plots. Later, a neighboring colony that was also released from interspecific competition excluded colony 13 foragers from part of their original territory. The *P. mayri* numbers in both foraging plots rose significantly (*t* test, $P < .01$). For example, in the plot originally outside the territory, no *P. mayri* were found in 3 days before removal of the *E. ruidum,* 10 were found the day of removal, and 56 on the fifth day after. The same pattern occurred in plot B, with the increase in *P. mayri* coming from the neighboring nest. It is clear from these results that *E. ruidum* severely restricts the foraging of *P. mayri* and therefore also affects the location, size, and shape of *P. mayri* territories.

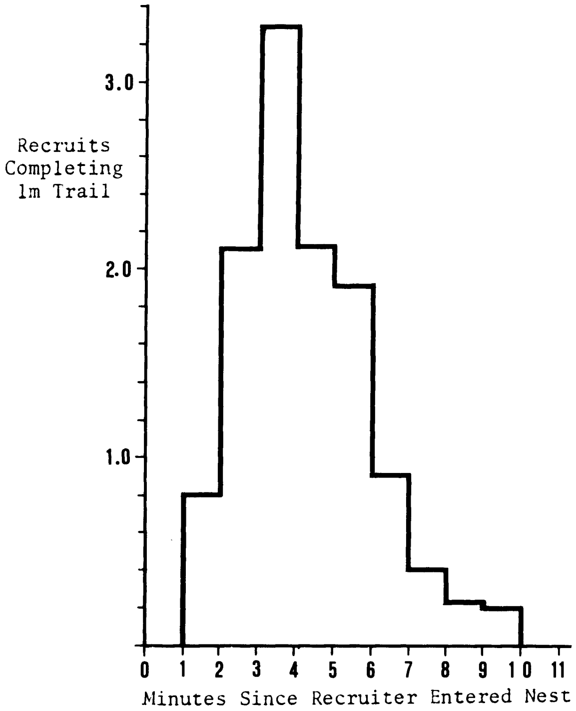

FIGURE 7. Duration of effectiveness of the trail pheromone in field conditions. Recruits arriving at a bait site each minute were counted; the graph shows the average of 25 trials. The decline in recruitment with time shows that recruits do not reinforce the trails they follow.

FORAGING.—*P. mayri* foragers return to the nest in more or less straight lines, except to circumvent obstacles. Since these ants tend to avoid areas of deep leaf litter and rarely climb more than 5 cm up a vertical surface, the paths of foragers frequently converge around even small rocks, logs, or vegetation, giving the false appearance of branching trunk routes (Fig. 3). Maximum foraging distance from the entrance averaged 4.7 m (range = 2.0–9.4 m, SD = 1.6 m). When foragers find food, they do not consume it in the field, but instead individually carry or drag it back to the nest. There was little cooperation among foragers either to cut food into smaller pieces or to transport large items.

Recruitment to new food sources is at least partly organized by a trail pheromone. When the path of a first recruit was compared to the incoming path of a baited and marked forager, 24 out of 25 times there was exact correspondence for the entire 1 m length. In the three control tests as well, the recruits followed the recruiter's incoming path, rather than the diverging line of twigs. For the three recruiters that did use the same inbound and outbound paths, the inbound path was also the straightest path to the nest. Of the 25 recruiters, however, 22 returned to the bait site by a different, usually straighter path, ignoring their own trail until arriving at the site. Not finding food, they searched until they located their trail, then followed it to the bait site. The trail pheromone of *P. mayri* is very short lived and is not reinforced by outbound recruits (Fig. 7). In the tests described so far, both recruits and recruiters were collected as they arrived at the bait site. On two other occasions, when ants were allowed to return to the nest after being recruited to the bait, I noted that at least some did not follow the chemical trail on their returns to the nest. These observations suggest that other means of orientation are employed to continue visiting a food source, once a recruit is led to the food by a chemical trail.

The sluggishness of *P. mayri*'s recruitment system is further demonstrated by an experiment with one nest in which large, continually replenished caches of peanut chips were placed at 1 m and 4 m from the nest entrance. Recruitment at both sites reached an asymptote of 18 ants/5 min after one hour, and stayed at about that rate for the next hour. Foraging intensity may have been affected by the presence of *E. ruidum,* but *P. mayri* retained dominance over the baits. Even with a persistent food supply, *P. mayri* never develops a narrow trunk trail. Instead, foragers may be found anywhere within a concourse about 10–30 cm wide.

A forager apparently confines its activities to one sector of the territory unless recruited elsewhere. Figure 8 shows typical results of marking workers in one sector, then in subsequent days mapping the positions of all workers throughout the territory. Three such tests were performed with different nests. By the fifth to seventh days after marking, 77 percent of all marked ants ($N = 35$) were still in the sector subtended by the area in which they were marked (mean marked ants per territory = 17.6; mean per sector = 13.7, SD = 5.2). Most of the others were in adjacent sectors. A baiting experiment in one of these territories showed that foragers can be recruited to long-term food supplies in other sectors.

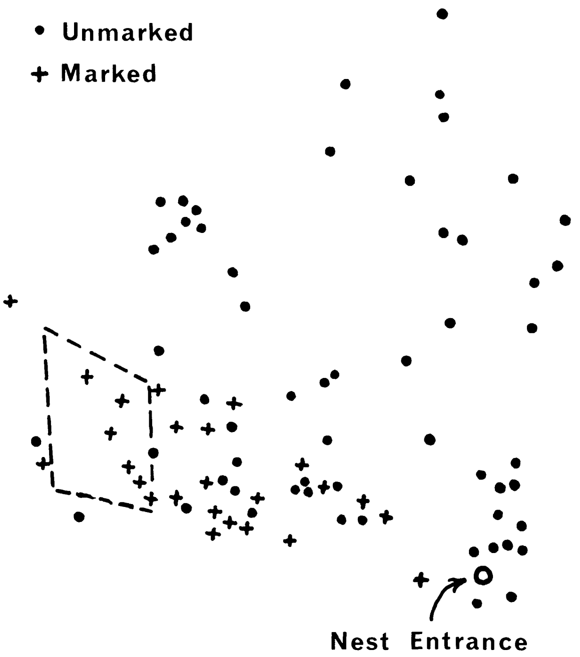

FIGURE 8. Results of a forager constancy experiment. Ants were marked in the trapezoidal area, then later the positions of all marked ants (+) and unmarked ants (−) were mapped. This is a cumulative result of four censuses taken 5–7 days after marking.

## DISCUSSION

*Pogonomyrmex mayri* is an obligately diurnal forager, but during the day timing and direction of foraging is variable and largely dependent on temperature. In the rainy season and at well-shaded sites during the dry season, when temperatures on the ground remained below 34°C, foraging peaked at midday. In the dry season, foraging continued in shaded portions as long as the nest entrance itself remained in shade. Colonies with fully exposed entrances and territories ceased activity, or nearly so, for several hours at midday when ground temperatures exceeded 38°C. Since the North American *Pogonomyrmex* live in grasslands or desert, rather than in forest like *P. mayri,* this midday estivation is commonly observed (Cole 1934, Golley and Gentry 1964, Willard and Crowell 1965, Rogers 1974). Unlike *P. mayri, P. rugosus* and *P. barbatus* can facultatively forage at night (Whitford and Ettershank 1975, Whitford *et al.* 1976).

Intraspecific competition also can severely limit the distance and direction of foraging. Each colony maintains a foraging territory, and the territories are often surrounded by no ant's lands in which about 78 percent of the encounters between neighbors are overtly aggressive and occasionally injurious. If territories overlap, the smaller colony is forced to leave. Removal of a colony results in the invasion of that area by a neighboring colony. Strong intraspecific competition explains the overdispersion of *P. mayri* nests (Levings and Traniello 1981, Kugler and

Hincapié 1983). Intraspecific competition has been demonstrated in *P. rugosus, P. barbatus, P. maricopa,* and *P. californicus* (Hölldobler 1976, De Vita 1979).

Interspecific competition is often inferred from dispersion analyses or from exclusive temporal or geographic distribution of species (Whitford *et al.* 1976, Davidson 1977, Byron *et al.* 1980), but Hölldobler (1976) gave direct evidence of the effect of competition between two very closely related species, *P. rugosus* and *P. barbatus.* Competition between those two species and a species less similar in diet and foraging, *P. maricopa,* was shown to be less intense, but *P. maricopa*'s effect on the distribution or abundance of the other two species and vice versa was not established. The effect of competition between distantly related species is clearly seen in this study of the interaction between *P. mayri* (Myrmicinae) and *E. ruidum* (Ponerinae). The niche of *E. ruidum* broadly overlaps that of *P. mayri.* Removal experiments demonstrate that *E. ruidum* can completely prevent *P. mayri* foraging in areas well within *P. mayri* foraging range and microhabitat, but in turn *E. ruidum* is prevented from foraging heavily in the vicinity of a *P. mayri* nest entrance. The competitive inhibition is not equal; *E. ruidum* has a much greater effect on *P. mayri.*

One possible explanation for *P. mayri*'s poor competitive ability is its weak recruitment ability. Each forager normally limits its searching to a single sector of the territory. When it finds food, it deposits a chemical trail as it returns to the nest. A few recruits can follow the ephemeral trail to the food before the pheromone evaporates, but they apparently do not follow the trail back to the nest. Moreover, the recruiter generally does not follow its own trail on its return to the food. I surmise that only new recruits follow a chemical trail, and once the location of a food supply is learned, they rely on some other as yet undetermined means of orientation to guide them to and from the nest. This could explain why even with a constant food supply, trails never become narrowed to a single file.

All *Pogonomyrmex* analyzed so far recruit with a trail pheromone produced in the poison gland and deposited by the sting of a returning worker (Hölldobler and Wilson 1970, Hölldobler 1976). Unlike *P. mayri, P. badius* recruiters apparently do follow their own trails from the nest back to a food source (Hölldobler and Wilson 1970). Group foragers like *P. rugosus* and *P. barbatus,* which form distinct columns, can forage farther and recruit faster than individual foragers like *P. maricopa* (Hölldobler 1976). *Pogonomyrmex mayri* is an individual forager with an even shorter foraging range and slower recruitment rate than *P. maricopa.* That may be due to its smaller colony size (Kugler and Hincapié 1983), but it may also be due to an even weaker reliance on trail pheromones. Further investigations on the orientation and recruitment methods of *P. mayri* and other less specialized *Pogonomyrmex* are necessary. Since *Pogonomyrmex* is one of the more primitive myrmicine genera, the findings of such studies may provide insights into the evolution of trail following in the Myrmicinae.

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