Home Range Orientation and Territoriality in Harvesting Ants  
(*Pogonomyrmex*/aggressive confrontation/foraging behavior)

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ABSTRACT Trunk trails, used by *Pogonomyrmex 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*.

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. Since Elton's (1) first documentation of the phenomenon in *Formica rufa*, intra- and interspecific territoriality has been described in a number of ant species (see refs. 2, 3). Most of these studies have been concerned with the ecological aspects of territoriality. Very little has been learned about the behavioral basis of territorial organization and orientation within the home range. The problem for the ants becomes especially acute when several closely related species coexist at high population densities.

This article reports for the first time some of the basic behavioral mechanisms used by *Pogonomyrmex*, the most abundant and specialized genus of harvesting ants in North America (4), in establishing and maintaining its foraging territories.

Spacing and trunk trails in *Pogonomyrmex*

Our study area in Arizona, near the Southwestern Research Station (Portal), is densely populated with nests of at least five *Pogonomyrmex* species. We concentrated on three, *P. barbatus*, *P. rugosus*, and *P. maricopa*, which seem to have overlapping food preferences. A preliminary survey indicates that *P. barbatus* and *P. rugosus* use the same resources for food and nesting sites, whereas *P. maricopa* may be somewhat specialized for occupying less vegetated sites and collecting smaller seeds. The daily activity rhythm of the three species is very similar.

In most habitats the *Pogonomyrmex* colonies are fairly regularly spaced, a common sign of territorial behavior in other groups of animals. In our study area *P. maricopa* is considerably more widely spaced (mean distance 46 m) than *P. barbatus* (18 m) and *P. rugosus* (17 m). However, *P. maricopa* often nests relatively close to *P. barbatus* and *P. rugosus*, whereas the interspecific distance between *P. barbatus* and *P. rugosus* is almost the same as the distance separating nests of the same species.

Another 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 most of the foragers from *P. barbatus* and *P. rugosus* colonies travel on well established trunk trails before diverging on individual excursions. After foraging, the *barbatus* and *rugosus* workers return to these routes for the journey home. Such trunk trails sometimes extend for more than 40 m; they are remarkably persistent over long periods of time and even survive heavy rainfall.

Employing a cartographic survey of the three species in two sections of our study area, we compared spacing patterns, foraging ranges and trunk trails (Figs. 1 and 2). The following conclusions and inferences were drawn:

1. Trunk trails of intraspecific neighbor nests never cross. On the contrary, they regularly diverge as though the trail-laying workers had been repulsed from preexisting trails.

2. When workers leave the tracks and disperse on individual seed-collecting trips, they occasionally meet workers of neighbor colonies of the same species. This invariably leads to fierce fighting that frequently ends in severe injury or death for both. Such encounters usually occur only between pairs of ants. Mass confrontation is evidently avoided by keeping the trunk trails far enough apart.

3. Trunk trails of interspecific neighbors (*P. barbatus* and *P. rugosus*) are usually also clearly separated. However, they approach closer than those of intraspecific neighbors. Individual encounters between *P. barbatus* and *P. rugosus* are as aggressive as intraspecific encounters.

4. *P. maricopa* has no trunk trails. Individual workers forage out up to 25 m in all directions around the nest. They run across the tracks of *P. barbatus* and *P. rugosus*. Individual 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 their respective foraging ranges, prolonged, heavy fighting typically ensues. As can be seen from Fig. 2 such fighting zones, which are identical to the territorial borders, are especially active when a younger colony (see Fig. 2, Nest no. 3) gradually grows and extends its territory already established territories of other colonies (Nests no. 2, 4, and 5 in Fig. 2). It is apparent in the example shown that colony no. 3 was destined eventually to be pushed out of its nesting and foraging area.

5. The lack of a trunk trail system apparently compels colonies of *P. maricopa* to space out over much larger distances than those of *P. barbatus* and *P. rugosus*. Trunk trails appear to be devices to avoid mass confrontations between neighboring colonies of the same species. They channel the mass of foragers of hostile neighbor colonies into diverging...
directions, before each ant pursues its individual foraging exploration. This foraging technique ensures a more effective partitioning of the foraging grounds and allows a much denser nest concentration 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 more sparsely populated habitats.

**Experimental analysis**

Laboratory experiments suggest that trunk trails originate from former recruitment trails. As shown in earlier reports, the recruitment intensity (number of ants laying a trail) depends on the density of the “seed fall.” The larger the amount of seeds per unit area the more intense the mass recruitment activity. More enduring chemical sign posts are also deposited along the recruitment trails. The latter substances function as orientation cues, so that long after the recruitment signal has vanished, motivated foragers can still follow the same track (5-7).

Additional experiments have been devised to test the hypothesis that trunk trails function at least in part to partition the foraging grounds with a minimum of hostile confrontation between neighboring colonies. Only a single representative experiment will be described here (see Fig. 3). We first laid a “seed line” between two close neighbor colonies of *P. barbatus*. Workers of both nests quickly began to carry the seeds homeward, thus “rolling up” the seed line from both ends. When both foraging groups met we then provided new seeds *ad libitum* at the meeting point. This procedure intensified the recruitment behavior and led to a severe battle. Within the next four hours 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.” Up to this time at least 300 ants had been killed by intraspecific fighting and the conflict continued even after we stopped providing seeds.

Three days later the two trails were seen to be diverging. Colony A (Fig. 3) still used the newly established trunk trail,

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**Fig. 1.** Map of the colonies and their foraging areas in one section of our study site in Arizona. ○, *P. maricopa* nest; ♂, *P. rugosus* nest; ♂, *P. barbatus* nest; ♂, *P. rugosus* or *P. barbatus*; ○, intraspecific fighting *P. rugosus*/*P. barbatus*; X, intraspecific fighting *P. maricopa*.
whereas Colony B had changed its route by about 40° to the west. Further experiments in the field clearly demonstrated that topographic cues are responsible for stabilizing such course changes of trunk trails. This is demonstrated, for example, with the striking example illustrated in Fig. 3. Before separation of the trunk trails the route of Colony B passed

![Map of relatively closely spaced P. maricopa colonies and their intraspecific fighting zones. P. rugosus nests in the immediate neighborhood are also illustrated. •, Intraspecific fighting, P. maricopa; ○, Interspecific fighting, P. maricopa/P. rugosus.](image)

**Fig. 2.** Map of relatively closely spaced *P. maricopa* colonies and their intraspecific fighting zones. *P. rugosus* nests in the immediate neighborhood are also illustrated. •, Intraspecific fighting, *P. maricopa*; ○, Interspecific fighting, *P. maricopa/P. rugosus*.

![Schematic illustration of a field experiment demonstrating that trunk trails are established as an outcome of the recruitment process.](image)

**Fig. 3.** 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. At this meeting point we continued to offer seeds. This led to heavy fighting between workers of A and B (○).
3. After we stopped providing seeds, the tracks began to diverge.
4. By removing a conspicuous landmark (bush), it was found that the change in the course of trunk trail B had been stabilized by this landmark.
a bush at the left side. After the course of the track had been changed it passed the bush at 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 sharply increased again. This and similar results suggest that the dominant chemical signals along the trunk trails are supported by visual orientation cues such as nearby conspicuous landmarks. Such facilitation of course requires that the ants acquire an intimate familiarity with these visual cues in the course of following the chemical trails. By extensive marking experiments we could indeed demonstrate that Pogonomyrmex shows a high trunk trail fidelity. For example, of 400 P. barbatus workers marked on one trunk trail, only five ants were seen during the next 3 weeks leaving the nest on another track. A similar high route fidelity, based on visual cues, has recently been reported for several species of the ant genus Formica (8).

Conclusions

The use of chemically 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 in dense vegetations or during the night. In southern Arizona P. rugosus shows a nocturnal foraging activity during the hottest part of the summer. We found that the nocturnal foragers depend heavily on their chemically marked trunk trails for precise home range orientation.

It is interesting to compare briefly the trunk-trail foraging strategy of P. barbatus and P. rugosus with the more individualistic foraging behavior of P. maricopa. Although P. maricopa occasionally uses short-lived chemical recruitment trails to attract nestmates to rich food sources, experiments in the laboratory as well as the field revealed that individual ants are guided principally by visual cues. This foraging and orientation strategy obviously does not allow as precise a partitioning of foraging grounds as the trunk trail strategy. This explains why P. maricopa colonies are much more widely spaced than those of P. barbatus and P. rugosus. If a future quantitative analysis of the food preferences of these three Pogonomyrmex species confirms our suspicion that P. maricopa is more specialized in its food preferences than P. barbatus and P. rugosus, then the adaptive significance of a wider spacing pattern of P. maricopa populations will have become apparent.

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