Nest Relocation in Harvester Ants

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ABSTRACT It has been suggested that colonies of the genus *Pogonomyrmex* relocate their nests in response to crowding by neighboring colonies. Nest relocations and distances moved were observed in a population of about 250 colonies of *Pogonomyrmex barbatus* (F. Smith). Nest relocation tends to occur after summer rains. 20% of colonies attempt to relocate nests each year, and half of these, or 10% of the population, complete the move. These data indicate that the stimulus to move may be different from the factors that ultimately determine the suitability of a new nest site. There was no relation between distance to the nearest neighbor and tendency to move, or between colony age and tendency to move. Certain colonies are likely to move year after year. It is possible that colonies relocate in an unsuccessful attempt to escape infection or infestation that is transferred when they move.

KEY WORDS Insecta, *Pogonomyrmex barbatus,* intraspecific competition, nest relocation

THERE HAS BEEN CONSIDERABLE interest in the spacing patterns of sessile organisms and the effect of competition on such patterns (Levings & Traniello 1981, Pacala & Silander 1985, Ryti 1991). In ants, distance between nests is sometimes used as a measure of the intensity of competition for food (Ryti & Case 1986, Cushman et al. 1988); nests that are closer together are assumed to compete more strongly. Competition for food limits the populations of desert seed-eating ants (Brown & Davidson 1977, Davidson 1985). In seed-eating ants, it has been suggested that if a *Pogonomyrmex* colony becomes too crowded by its neighbors, it moves (DeVita 1979, Harrison & Gentry 1981); this has been observed in other ant species (Bradley 1972). Although intraspecific competition may lead to randomly or evenly dispersed nest distributions (e.g., Levings & Traniello 1981), a long-term study of *P. barbatus* showed that distributions are neither stable nor evenly dispersed. Instead, distributions change from one year to the next as colonies die and new ones are founded, and distributions tend to be either random or clumped (Lo 1989, Gordon 1991). But colonies frequently relocate their nests. Here I examine the relation between nest relocation and the distribution of nest sites to see whether distance to conspecific neighbors influences the probability that a colony will move.

Materials and Methods

The locations of all *P. barbatus* nests in an 8-ha site in the Chihuahan desert near Rodeo, N. Mex., were mapped each year from 1985 to 1989 as described by Gordon (1991). Map locations were accurate to about 0.5 m. All colonies were checked five to eight times each summer to determine if nest relocation was taking place. Observations were made at about weekly intervals through July and August. Nest relocations have been observed every year since 1981, and distances moved were measured in 1987, 1988, and 1989.

Results

The surface of a *P. barbatus* nest is a cleared disk or mound, covered with pebbles, containing one to three entrances. When a colony attempts a move, one to five new nest entrances are constructed 1–10 m from the edge of the existing nest mound. Nest construction takes several days. A colony may construct new nest entrances and then not move at all; I refer to this as an "aborted move." Other attempted moves are eventually completed, and the entire colony relocates to the new nest (a "completed move"). When a move is completed, one new nest entrance is chosen, and workers, callows, brood, and queen are moved into it in 1 d (sometimes 2 d) at the end of the morning activity period. Several days later, workers can still be seen retrieving stored seeds from their old nest. In one case, workers were seen taking seeds from the abandoned nest of a conspecific neighbor that had recently moved. In the course of a complete move, a colony also takes some of the small pebbles used to cover the surface of its old nest mound to the new nest and sometimes takes them from the nests of other colonies that have

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Table 1. Colony-specific tendency to move; colonies that move one year are likely to move the next[a]

Year and nest relocation	Moved	Did not move
	1988	
Moved in 1987	7 (2.6)	7 (11.5)
Did not move in 1987	18 (22.4)	104 (99.6)
	1989	
1988–1989		
Moved in 1988	14 (4.8)	11 (20.2)
Did not move in 1988	12 (21.2)	99 (89.8)

[a] Observed numbers of colonies in each category are shown first; expected values are shown in parentheses.

died. While a colony is completing a move, it does little or no foraging.

About 10% of all colonies >2 yr old relocate each year. In 1987, 17 of 142 colonies moved (11%); in 1988, 19 of 207 (9%); and in 1989, 25 of 302 (8%). Colonies that completed moves in 1988 moved a mean distance of 8.3 ± 1.98 m ($\bar{x}$ ± SD); in 1989, the mean distance moved was 7.1 ± 4.31 m. Some colonies constructed new nest entrances on mounds abandoned by other colonies at least 1 yr before (e.g., 20% of all colonies that completed moves in 1989 did this). Large, abandoned *P. barbatus* nests are sometimes occupied by another granivorous ant, *Novomessor (=Aphaenogaster) cockerelli* (E. Andre).

Aborted moves are common. In 1988, there were 29 attempted moves, including in three cases >1 attempt by the same colony. Of the 29, 18 were completed (62% completed, 38% aborted); in 1989, of 52 attempted moves, 25 were completed (48% completed, 52% aborted). There were no discernible differences between nest entrances that were constructed but abandoned and those into which a colony eventually moved. It appears that some factors, such as crowding or unsuitable nest conditions, cause a colony to attempt to move, whereas other factors, such as fighting with neighbors near new nest sites, determine whether the move is completed. In the following account, when examining the factors that may instigate an attempt to move, I pooled counts of attempted and completed moves.

Certain colonies tend to move, or attempt to move, year after year. I tested this hypothesis using data for 136 colonies present in 1987, 1988, and 1989. Here, only colonies that were alive and mapped in all 3 yr were counted, and both attempted and completed moves were counted. Of 14 colonies that attempted or completed moves in 1987, 7 (50%) did so again in 1988. Of 26 colonies that completed or attempted moves in 1988, 14 (54%) did so again in 1989. A two-way table was constructed comparing the number of colonies that moved and the number that did not move in 1 yr, with the number that did and the number that did not move the next (Table 1). A χ^2 test was used to test whether the proportion of colonies that completed or attempted moves 2 yr running was significantly larger than expected. Colonies that completed or attempted to move one year tended to do so again the next, both from 1987–1988 ($\chi^2 = 8.2$, $P < 0.01$) and from 1988–1989 ($\chi^2 = 24.1$, $P < 0.001$).

Moves seem to occur after a period of heavy rainfall. Either moving is a response to flooding of the nest interior, or moving for other reasons must wait until after heavy rain. Because the hard calichi layer of the soil is difficult to penetrate when it is dry, it is probably easier to build a new nest when the soil is wet. In 1988, most colonies that attempted or completed moves (26 of 29) began the construction of new nests on the same day (11 August) after there had been 12 d of heavy rain in the preceding 4 wk. In 1989, a first wave of move attempts occurred 26–31 July, after 7 d of heavy rain in the preceding 4 wk; this wave involved 52 colonies, of which 27 made aborted moves and 25 completed moves. A second wave, of which all were aborted, occurred 17–22 August after 5 d of heavy rain since 1 August, involving 16 more aborted moves by 11 colonies that had done the same in the first wave, 3 colonies that had completed a move in the first wave, and 2 colonies that had not attempted moves before.

New nest entrances were constructed on existing foraging trails. In 22 of the colonies that attempted or completed moves in 1989, foraging trails had been mapped in the week preceding the move. In 17 of these 22 colonies, all new nest entrances were constructed on foraging trails; in 2 other colonies, at least one new nest entrance was on a foraging trail; in 3 other colonies, new entrances were not on a trail. Thus, new entrances not on a trail were unlikely (3 of 22, by binomial test; $P < 0.001$).

A colony's tendency to move did not depend on its age. As it gets older, a colony grows in size, or numbers of workers, so age may be used as an approximate, if imperfect, estimate of size. Using yearly maps made since 1981 and measures of nest size, all colonies on the study site were assigned an age in 1985 (techniques described by Gordon [1987, 1991]) and in every subsequent year. Colonies 2 yr or younger were omitted from the following test, because data on moving for very young colonies are not reliable: their nests often appear and disappear from one week to the next (which nests of older colonies never do), making it difficult to distinguish a relocation from the death of one colony combined with the emergence of another. Colonies aged 3–9 yr in 1989 were divided into those that did not attempt moves, aborted moves, and completed moves. The 9-yr-old colonies were those determined to be at least 5 yr old in 1985; they may have been older. There was no relation of colony age and its tendency to move (ANOVA, df = 2, 156; SS = 1.94; $F = 0.23$; $P > 0.79$). (For this ANOVA and others discussed below, inspection of the residuals showed that the data met the assumptions of the ANOVA.)

If colonies move when they are crowded, nearest-neighbor distances for colonies that move would tend to be smaller than those for colonies that do not move. It may be that colonies can move only after rain, and rains are heaviest in the summer. This means there may be a lag of up to a year between the occurrence of interactions with neighbors that could cause a colony to move and the time, during and after summer rains, that a colony actually can move. In testing for the relation between nearest-neighbor distances and nest relocation, both recent and year-old nearest-neighbor distances were considered. (Nearest-neighbor distances differ each year because some colonies die and new ones appear.) Using the relocation data from 1989, a one-way ANOVA was performed using the nearest neighbor distances after moves in 1988 for colonies that did not attempt to move, colonies that aborted moves, and those that completed moves. A second, similar ANOVA used nearest-neighbor distances just before moves in the summer of 1989. I also compared the nearest-neighbor distances before and after moves of the colonies that completed moves in 1989, using a paired two-tailed t test.

The results show no relation between nearest-neighbor distances and nest relocation. There were no significant differences among nearest-neighbor distances in colonies that moved, that attempted but did not complete moves, or that did not attempt to move at all. This was true in the analysis using nearest-neighbor distances from the year before (1988) (in feet) (ANOVA, SS = 485.3; df = 2, 167; $F = 0.89$, $P < 0.40$) and in the one using those from the same year (1989) (ANOVA, SS = 690.7; df = 2, 174; $F = 0.85$; $P < 0.43$). In 1989, the mean nearest-neighbor distance of colonies that moved was 8.74 ± 3.95 m before moves and 9.2 ± 4.6 m when moves were completed. There was no significant difference between nearest-neighbor distances before and after moves ($t = -0.518$, df = 22, $P < 0.61$).

Discussion

Relocation by *P. barbatus* does not seem to be caused by, or to change, proximity to a nearest neighbor of the same species. It appears that the function of relocation is not to adjust the distances between nests of the same species. The colonies observed in the present study are somewhat more crowded than colonies of the same species observed elsewhere. The average distance from a colony to its nearest neighbor ranged from 10.8 to 12.9 m over 4 yr ($n = 74–178$) (Gordon 1991); other authors have reported larger average nearest-neighbor distances (e.g., 18.1 m, $n = 35$ [Hölldobler 1976]). However, the proportion of colonies here that move (about 10%, $n = 142–302$ in 1987–1989) is smaller than those reported previously for *P. barbatus* (24%, $n = 25$ [Van Pelt 1976]) or *P. badius* (40–100%, $n = 10$ [Gentry 1974]). The larger proportions previously reported could be due to sampling error from much smaller sample sizes. But if it is true that fewer colonies move when all are more crowded, this further supports the conclusion that crowding does not cause relocation.

Certain colonies tend to move year after year. This suggests that nest relocation may be a reaction to some condition that colonies carry with them when they move. One possibility is a parasitic infection. Another is fungal infection, such as the *Aspergillus* that afflicts *P. rugosus* Emery (Gillam et al. 1990). Individuals live only a year (Gordon & Hölldobler 1988), and younger workers might attempt to move away from older, infected ones. It may be that colonies move because nest conditions deteriorate in some way (e.g., Van Pelt 1976), but this would suggest that certain colonies tend to construct inadequate nests or consistently fail to maintain them.

It is interesting that summer rains, relocation, widespread fighting between colonies, and the period of mating flights and colony founding all seem to occur within the same period of several weeks (unpublished data). Both relocation and colony founding may require wet soil for the construction of new nests. Fighting may be stimulated by the territorial changes generated by relocation and by the appearance of the nest entrances of founding queens (Rissing & Pollock 1987, Hölldobler & Markl 1989). Colonies constructed new nest entrances on their own existing foraging trails, as reported previously for *P. barbatus* (e.g., Van Pelt 1976) and *P. badius* (Latreille) (Harrison & Gentry 1981); foraging trails are the site of interactions with conspecific neighbors (Gordon 1991). The presence of conspecific neighbors may affect the choice of new nest sites, possibly after other factors have instigated the initial attempt to move. Finally, the effects of interactions with adjacent colonies of other seed-eating ant species remain to be investigated; for example, *P. maricopa* Wheeler is common on the study site.

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