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Ants distinguish neighbors from strangers

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Summary. Ants are known to distinguish their own nests and nestmates from all others, using colony-specific odors. Here I show that harvester ants (*Pogonomyrmex barbatus*) can further distinguish between two kinds of non-nestmates of the same species: neighbors and strangers. Interactions between colonies were thought to depend on the numbers of alien ants that each colony encounters on its territory. The results described here show that such interactions also depend on information about colony identity. Encounters on foraging trails with ants from neighboring colonies, deter foraging more than encounters with ants from distant ones. The history of interactions between particular pairs of colonies may have important effects on intraspecific competition for food.

Key words: Intraspecific competition – Seed-eating ants – Neighbor recognition

Harvester ants are part of a guild of granivorous species, including birds and rodents, all of which compete for seeds in desert communities (Brown and Davidson 1977). There is considerable evidence, both demographic (Davidson 1977) and behavioral (DeVita 1979; Holldobler 1976; Gordon 1988) for intra- and interspecific competition among ants of the genus *Pogonomyrmex*. Distribution patterns (Whitford et al. 1976; Davidson 1977) and behavioral observations (Holldobler 1976) suggest that density-dependent intraspecific competition is strong among *P. barbatus* colonies.

Earlier work had suggested that neighboring colonies avoid each other in order to prevent massive, and energetically expensive, fighting (Holldobler 1976); this appears to be the case in other seed-eating species (Harkness and Isham 1988). But recent work (Gordon unpublished work) shows that trails of neighboring *P. barbatus* colonies frequently intersect. After such encounters, whether a colony continues to forage in the direction of a neighbor's trail depends on the amount of food resources to be gained. Colonies that have lived in proximity to each other for more than five years tend to avoid encounters, while encounters between recent neighbors are often prolonged. This raises the possibility that competitive interactions depend not only on the number of alien workers that a colony encounters, but also on the history of interactions between particular colonies. That is, intraspecific territorial behavior may be based on information about colony identity.

Territorial behavior in ants depends on the ants' ability to distinguish their own nests and nestmates from all others, using colony-specific odors borne by each ant, and scent-marking cues placed on the ground and foraging trails (Holldobler and Lumsden 1980). Here I describe experiments that test whether ants distinguish neighbors from strangers. I compared foraging behavior after encounters with workers of conspecific, adjacent colonies, with foraging after encounters with conspecifics from more distant colonies. *P. barbatus* is monogynous and new colonies are started by mated queens that disperse at random from a distant, aggregated mating site. There is no correlation between relatedness and proximity; that is, there is no reason why adjacent colonies should be more closely related than more distant ones.

Methods

Experiments were conducted in the field, near Rodeo, New Mexico, USA. Each experiment involved counts of numbers foraging in three colonies, observed simultaneously. One colony was left undisturbed to control for changes in foraging intensity due to weather conditions, such as a cloud blocking the sun. In each of the two experimental colonies, 20 alien conspecific ants, neighbors or strangers, were placed on a foraging trail. In one experimental colony, the alien ants placed on the trail were collected from a neighboring (within 10 m, with potentially intersecting foraging trails) and adjacent colony. In the other experimental colony, the alien ants placed on the trail were collected from a distant colony more than 150 m away. Maximum foraging distances are about 40 m (Holldobler 1976), so workers from colonies 150 m apart would meet very rarely, if at all, when a lost forager from one colony happened to wander into the other's foraging territory. In each of the three colonies, 8 counts were made, at 5-min intervals beginning when alien ants were put down, of the numbers of foragers passing a point on the foraging trail in 10 s. Foraging intensity is a measure of the colony's reaction to the alien ants; harvester ants modulate foraging intensity in response to changes in the colony's environment (Gordon 1987).

Both neighbor and stranger ants were placed in similar plastic boxes when they were collected, and kept for similar lengths of time (about 20 min) until their simultaneous release. Because both neighboring and stranger ants were placed closer to the experimental nest than any conspecific alien ants usually go, both groups were equally in unfamiliar surroundings and there were no differences in the behav-

Table 1. Comparisons of foraging intensity. Nine experiments were performed on 9 different days. Each experiment included counts from three colonies: 1) undisturbed as control, 2) a colony exposed to ants from a stranger colony, and 3) a colony exposed to ants from a neighbor colony. The first 3 columns show, for each colony, the means of 8 counts, at 5-min intervals, of the numbers of foragers passing a point on the foraging trail in 10 s. In the next three columns, an '×' shows that pairwise interval-by-interval comparisons of counts for two colonies were statistically significant in the indicated direction ($P<0.05$, Wilcoxon signed-ranks test). If the same pair of colonies was used in more than one experiment, results for both are shown with an '×'

Date	Mean numbers foraging in 10 s			Pairwise comparisons of interval-by-interval counts		
	Controls	With strangers	With neighbors	Controls > strangers	Strangers > neighbors	Controls > neighbors
29-7	14.0	5.0	9.8	×		
30-7	10.0	7.3	4.6	×	×	
1-8	8.9	7.4	2.0	×	×	
2-8	6.5	9.8	4.1		×	×
3-8	5.4	4.9	1.6	×	×	
8-8	5.6	7.6	2.4		×	×
11-8	9.3	6.1	3.5	×	×	
12-8	6.6	4.0	2.6	×	×	
13-8	10.1	5.0	2.1	×	×	

ior of the two groups. In both cases, the released alien ants circled around, were inspected by foragers of the experimental colony, and then left the area.

Experiments were repeated 9 times on 9 different days using a total of 7 mature colonies (not including colonies from which ants were collected). Each colony was used at least once in each treatment (undisturbed, colonies exposed to neighbors, colonies exposed to strangers). The data were analysed in two ways. First, an ANOVA was performed, using the means of the 8 counts of foraging intensity for each colony in each experiment (shown in Table 1), testing for the effect of day and of treatment (undisturbed, exposed to neighbors, exposed to strangers). Second, within each experiment, 2 pairwise comparisons were made of the eight simultaneous counts using a Wilcoxon signed-ranks test: 1) between the undisturbed colony and the colony exposed to strangers, and 2) between the colony exposed to strangers and the one exposed to neighbors. If, within an experiment, the results of the Wilcoxon signed-ranks test showed the following inequalities to be statistically significant: counts for undisturbed colonies > counts for colonies exposed to strangers, and counts for colonies exposed to strangers > counts for colonies exposed to neighbors, it was concluded that counts for undisturbed colonies > counts for colonies exposed to neighbors. In the experiments for 2 August and 8 August, the first inequality did not hold, so the latter one was tested.

Results

Colonies react more strongly to encounters with ants from neighboring colonies than to encounters with ants from distant colonies. Ants from a stranger colony deterred foragers, relative to the controls. Ants from a neighboring colony deterred foraging even more. Figure 1 shows results of one experiment; all results are summarized in Table 1. There was no significant day effect (df = 8, 16; $F=1.89$, ns). There was a highly significant effect of treatment (df = 2, 16; $F=11.92$, $P<0.001$). In 6 of 8 independent (using different pairs of colonies) trials, colonies exposed to ants from stranger colonies foraged less than control colonies (Wilcoxon signed-ranks test, $P<0.05$). In 7 of 8 independent trials, colonies exposed to neighbors foraged less than colonies exposed to strangers (Wilcoxon signed-ranks test, $P<0.05$).

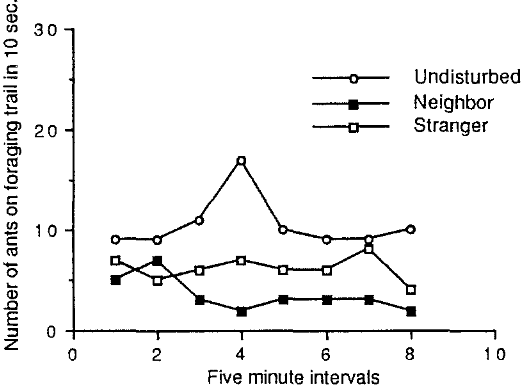

Fig. 1. Neighbors deter foraging more than strangers do. The figure shows data from one experiment

Discussion

The mechanisms of kin recognition are of central importance to kin selection (Hepper 1986). The problem is to find the cues that an individual uses to distinguish between members of its own kin group (i.e. nestmates, in ants) and unrelated individuals (i.e. non-nestmates) (Sherman and Holmes 1985; Holldobler and Carlin 1987). In ants, phenotype matching is based on odours derived from shared food and conditions, or passed on from the queen by grooming, and from genetically determined odors shared by all the queen's offspring (Holldobler and Michener 1986; Carlin and Holldobler 1986). But the neighbor-stranger discrimination reported here requires more than simple phenotype matching because an ant distinguishes between two different kinds of conspecific ants unlike itself. An ant can recognize not only "self" and "other" but particular types of "other".

It seems likely that some learning or "association" mechanism (Holldobler and Carlin 1987) accounts for neighbor recognition. In laboratory experiments, ants are more likely to accept non-nestmates after the two colonies are maintained in proximity (Obin 1986), which suggests that learning plays a role in intra-colony discrimination. But environmental cues alone do not provide a satisfactory explanation for the present results. This explanation would entail an implausible sequence: instead of a continuum of responses to a gradient of environmental cues, ants would have to accept others from a very similar environment (nestmates), be deterred by those from a fairly similar one (neighbors), and then react *less* strongly to those from a very different one (strangers).

What factors might lead to the evolution of neighbor-stranger discrimination? Birds distinguish the songs of neighbors and strangers, but, in contrast to the results described here, birds react more strongly to the songs of strangers than to those of neighbors (Falls 1982; Falls and Brooks 1975). The "dear enemy" effect (Wilson 1975) was suggested to account for the evolution of neighbor-stranger discrimination in birds: once territorial boundaries have been established, a bird has less to fear from its neighbors, with whom territorial relations have stabilized, than from a strange bird passing through in search of a new territory. Recent work shows that territorial conflict on intersecting foraging trails of neighboring harvester ant colonies is frequent, and can be mild enough to be sustained for long periods of time (Gordon unpublished work). Eventually colonies move or die out in response to crowding (Harrison and Gentry 1981; DeVita 1979), but relations between neighboring colonies are far from stable. When *P. barbatus* colonies do move, it is usually for distances <10 m (Gordon unpublished work). Colonies do not invade each others' nests. Strange ants from distant colonies encountered in a colony's territory are probably lost foragers, and do not presage an invasion of the nest or territory by the distant colony. The present results provide support, from a different phylum, for the "dear enemy" hypothesis by confirming its obverse. A colony has more to fear from its neighbors, with whom it competes for food, than from strangers. Thus it reacts more strongly to neighbors than to strangers.

P. barbatus workers live about six weeks after they enter the pool of exterior workers, which includes foragers (Gordon and Holldobler 1988). During this time, in the course of repeated encounters, foragers may learn the colony-specific odors of their neighbors. Foragers' fidelity to one trail, leading past certain neighboring colonies, may allow colonies to distinguish different neighbors according to their usual location. It may be that information about the odors of neighbors is passed from foragers or patrollers to other workers (Gordon 1989); we can now investigate how neighbor recognition develops in the lifetime of a colony. Neighbor recognition implies that colonies can deceive each other. A colony could deter a neighbor with the appearance of foraging, by sending a few ants on to the neighbor's trail, without actually having to deploy large numbers of ants. The possibility of neighbor-stranger discrimination raises many intriguing questions about the ecological consequences of long-term interactions between pairs of neighboring ant colonies.

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