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Deborah M. Gordon · Diane Wagner

Neighborhood density and reproductive potential in harvester ants

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Abstract When neighbors compete for resources, the characteristics of a neighborhood may affect fitness. We examined the relationship between reproductive success and the density and size/age characteristics of neighbors in a population of the seed-eating ant, *Pogonomyrmex barbatus*, in which the ages of all colonies were known. Reproductive success was estimated by trapping and counting the number of alate, reproductive ants emerging from the nest for the annual mating flight. Alate production was negatively related to neighborhood density. Decreased production of alates by more crowded colonies may be due to competition for food with surrounding colonies. Neighbor size/age was unrelated to alate production. If alate production is correlated with lifetime reproductive success, these results suggest that selection favors colonies that monopolize more space, whatever the size of neighboring colonies.

Key words Age-related effects · Density · Formicidae · Reproductive success · Spatial distribution

Introduction

The spatial distribution of a population is a consequence of birth and death processes. In turn, spatial distributions can influence those processes, since local density may affect an organism's chances of survival. Spatial distributions may also influence a population on the evolutionary timescale, when neighborhood effects help determine reproductive success (Antonovics and Levin 1980). In animal populations, such effects might shape the evolution of territorial behavior. If neighbors compete for resources that are linked to space, and reduced access to the resources entails reduced reproductive success, then natural selection might favor behavior that allows an individual to maintain its use of contested space.

Many species of seed-eating ants compete for food (Davidson 1977, Ryti and Case 1986). Local interactions among colonies are important because neighboring colonies must search contiguous or overlapping areas for food (Levings and Traniello 1981; Gordon 1992a). Density has a negative effect on survival of both newly founded colonies (Ryti and Case 1988a; Gordon and Kulig 1996) and established colonies (Wiernasz and Cole 1995) in seed-eating ants and in other ant species (Adams and Tschinkel 1995).

Here we investigate the relationship between neighborhood density and reproductive success in a population of the seed-eating ant, *Pogonomrymex barbatus*. Following standard practice (Keller 1993), we used the number of male and female alates as a measure of reproductive success. Like many ant species, *P. barbatus* reproduces only in an annual mating aggregation, composed of winged males and females, the alates, that have flown in from many colonies in the surrounding area. Newly mated queens fly away from the mating aggregation apparently at random; thus neighboring colonies are not especially likely to be related. Reproductives are larger and contain more fat than workers, and thus are more costly to produce (MacKay 1985). Food may limit alate production; manipulative experiments suggest this in some species (Ryti and Case 1988b) but not others (Munger 1992). It has also been shown that neighborhood density can negatively affect alate production (Pontin 1961; Ryti and Case 1988b).

Competition for foraging area in *P. barbatus* is linked to colony life history. Colonies are founded by a single queen. Colony size is correlated with colony age: a colony grows larger as it gets older, until it reaches a stable size of about 10,000 ants at 5 years (Gordon 1992a). Colonies live 15–20 years, until the founding queen dies (Gordon 1991). At about 5 years of age, a colony begins to produce alate, sexual forms (Gordon 1995). The foraging behavior of a colony, and its reaction to encounters with conspecific neighbors searching the same area for food, change as the colony grows older and larger (Gordon 1991, 1992a, 1995). Colonies of inter-

D.M. Gordon (✉) · D. Wagner
Department of Biological Sciences, Stanford University,
Stanford, CA 94305-5020, USA

mediate age, 3–4 years old, are more persistent than older, larger ones in returning to the site of a previous interaction with a neighbor (Gordon 1992a), but overall, large colonies (5 years or more) are most likely to overlap the foraging ranges of their neighbors (Gordon and Kulig 1996). The size of its neighbors may affect the ability of a colony to reproduce, because large neighbors compete more intensely than smaller ones for foraging area and thus for food.

This study was conducted in a population in which all *P. barbatus* colonies have been censused for 11 years, so that the age of all colonies is known or can be estimated. We measured alate production in focal colonies of similar age with neighbors that ranged from 1 to 14 years old. We estimated the effect of neighbour density and age/size on the alate production of a focal colony.

Materials and methods

Alate production was measured in a population of about 250 colonies in Rodeo, N.M. All colonies on the study site are of known age, having been mapped and censused each year since 1985 (Gordon 1991, 1992a; Gordon and Kulig 1996). Alates were collected in July 1995 in 45 colonies, all aged 5–7 years. We measured alate production in colonies of similar age, in the first few years of reproductive activity, to eliminate possible effects of variation in alate production due to queen senescence or other factors related to colony age. Though focal colonies did not vary much in age, the ages of their neighbors ranged from 1 to 14 years. We examined the effect of neighbor age, which is related to size (Gordon 1992a), on the alate production of focal colonies.

Two measures of density were used: (1) the distance to the seventh-nearest neighbor (the greater the distance, the lower the density), and (2) the number of colonies within a circle of 20 m radius. These measures were based on previous work, described below, showing that colonies are most likely to overlap in foraging range with their seventh-nearest neighbors, and that foraging ranges rarely overlap between colonies more than 20 m apart (Gordon and Kulig 1996).

The extent of overlap in the foraging ranges of neighboring colonies depends on neighbor size, and colony size is related to colony age. A young, small neighbor, aged 1–4 years, is only half as likely as an older, larger one, aged 5 years or more, to overlap the foraging range of another colony (Gordon and Kulig 1996). We tested the effect of neighbor size on alate production using, as a measure of neighbor size, the number of colonies within the nearest seven neighbors that were large colonies aged 5 years or older.

Alates were collected using cone-shaped traps made of aluminum screening, similar to those used by Munger (1992; personal communication) in which he caught 90% of the alates leaving the nest for the mating flight. A trap consisted of a circular base, with a radius of about 0.6 m, of wide screening about 8 cm high through which all ants, workers and alates, could pass freely. On this base was a large cone, 1 m high, of 1/4-inch hardware-cloth screening. This cone had an opening at the top, narrow end. A smaller screen cone, about 0.3 m high, was taped over the opening of the large cone. A small twig or piece of dried grass was placed leading from the nest entrance and up to the opening in the larger cone. On the day of the mating flight, alates emerged from the nest, climbed the twig and when they attempted to fly up, became trapped inside the smaller, upper cone.

Traps were secured around the nest mound of each focal colony 4 days before the mating flight, which took place on 20 July 1995. Because foragers could travel freely through the base of the trap, it did not affect the colony food intake. However, the raised base had an unforeseen consequence. During the mating flight, alates are attracted to the site of the mating aggregation, probably by chemical cues. In most years there is only one mating aggregation on the site, which usually occupies an area of 3–5 m^2 (Gordon and Kulig 1996). But females caught in our traps were apparently attractive to males, and aggregations formed on the ground around nine of the traps. In traps where there was no aggregation, most alates were sitting in the top cone, where they had apparently become caught when they attempted to fly away. In traps in the midst of an aggregation, however, there were also large numbers of alates on the ground underneath the trap. These alates were probably not from the colony under the trap but, rather, had run in under the base of the trap during the mating aggregation. Accordingly, data from the 9 colonies where an aggregation formed were omitted from the analysis, leaving data from 36 colonies where there was no aggregation.

The *P. barbatus* population studied here is the subject of a long-term study of population dynamics, which will continue in the future. For this reason, we sampled alates nondestructively. Alates were released from the traps as soon as possible and allowed to join the mating flight.

Results

Colonies at low density produced more alates (Table 1). There was a significant positive relationship between total number of alates and distance to the seventh-nearest neighbor (regression coefficient 1.073, $r^2 = 0.185$, $P = 0.009$, $n = 36$) (Fig. 1). Inspection of the residuals indicated that the variance was slightly higher at high distance to the seventh-nearest neighbor (low density), so the regression was repeated after transforming the *y* variate (total number of alates) by taking its square root. Again there was a significant positive relationship between the total number of alates and distance to the seventh-nearest neighbor (regression coefficient 0.148, $r^2 = 0.175$, $P = 0.01$, $n = 36$). The second measure of density, number of colonies within 20 m, led to similar results. In a preliminary regression of total number of alates on number of colonies within 20 m, inspection of residuals again suggested slightly higher variances at low density, so the total number of alates was again square

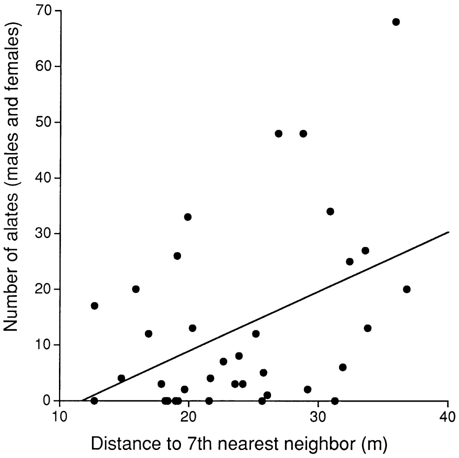

Fig. 1 Relationship of total number of alates to distance to the seventh-nearest neighbor. Each *point* shows the total number of alates (male plus female) for one colony. The *line* indicates the regression $y = 1.07x - 12.6$, $r^2 = 0.19$, $P = 0.009$

Table 1 Numbers of alates countded

Colony ID	Age in 1995	Number of Males	Number of Females	Distance to 7th nearest neighbor (m)	Number of colonies within 20 m	Number of 5-year olds among nearest 7 neighbors
269	7	9	4	10.3	1	7
271	7	3	0	7.4	2	3
289	6	5	0	7.9	2	6
295	7	25	1	5.8	7	5
308	7	10	10	4.8	9	7
310	7	16	11	10.2	1	6
311	7	0	0	6.6	5	7
313	7	4	0	4.5	8	7
326	7	0	0	5.8	7	7
340	7	0	0	5.6	8	6
348	6	30	4	9.4	2	4
352	6	0	0	3.9	12	7
360	7	45	3	8.8	5	7
368	7	3	0	7.2	3	6
374	6	12	0	7.7	3	5
390	5	15	2	3.9	14	5
433	7	0	1	7.9	3	7
436	5	2	6	7.3	3	7
447	7	0	0	7.8	6	7
448	5	1	1	8.9	5	7
455	5	1	2	5.5	7	5
460	5	7	0	6.9	5	6
464	5	0	2	6.0	7	5
469	7	28	5	6.1	7	5
470	7	41	7	8.2	2	6
472	5	0	0	9.5	3	4
480	7	9	11	11.2	1	5
484	5	3	1	6.6	5	3
501	5	8	4	5.2	7	5
508	5	0	0	5.5	8	6
511	5	12	1	6.2	6	4
522	6	5	1	9.7	2	7
537	5	0	0	5.9	7	4
538	6	46	22	10.9	1	5
551	7	0	0	5.6	10	5
583	5	15	10	9.9	4	6

root transformed. There was a significant negative relationship between the number of alates and the number of colonies within 20 m (regression coefficient −0.25, $r^2 = 0..09$, $P = 0.04$, $n = 36$).

Alate production was not affected by the number of old, large neighbors. There was no significant relationship between the total number of alates produced and the number of the seven nearest neighbors that were large colonies aged 5 years or more (regression coefficient −0.987, $r^2 = 0.005$, $P = 0.7$, $n = 36$).

Because female alates are considerably larger than males [about twice the dry weight in a closely related species, *P. rugosus* (MacKay 1985)], the production of females could be more constrained by food supply than that of males. On average, 29% of the alates produced were female (SD 29%, $n = 27$ nonzero counts). We found no evidence that the production of females was disproportionately affected by density. There was no significant relationship between the proportion of female alates produced and distance to the seventh-nearest neighbor (regression coefficient 0.007, $r^2 = 0.01$, $P = 0.6$, $n = 36$). Proportions were arcsin-square root transformed.

Discussion

Neighborhood density has a significant, negative effect on alate production in *P. barbatus*. This effect may be caused by competition for food. The closer two colonies are, the more likely they are to interact, indicating that density affects the extent to which colonies search the same foraging area (Gordon and Kulig 1996). At lower densities, when competition is less intense, colonies may have more food resources with which to produce alates. This result is consistent with studies of other species showing a negative relationship between local density and alate production (Pontin 1961; Ryti and Case 1988b), though experimental food supplements do not always lead to higher alate production (Munger 1992).

Alate production was reduced at high density for both measures of density we employed; distance to the seventh-nearest neighbor, and number of colonies within 20 m. Studies of foraging behavior in *P. barbatus* indicate that distance to the seventh-nearest neighbor probably reflects the extent of competition for foraging area more accurately than the number of colonies per unit area. Neighboring colonies meet when both search the same area for food (Gordon 1991, 1992a). A previous study tracked neighbor interactions in 34 colonies with local densities that ranged from 2 to 14 conspecific neighbors within 20 m (Gordon and Kulig 1996). Of 1,077 interactions, 75% were with one of the five nearest neighbors, and interactions were extremely rare with a neighbor more distant than the seventh-nearest one (see Gordon and Kulig 1996, Fig. 2). Each day a colony chooses from a set of habitual foraging trails (Gordon 1991); foraging area varies from day to day but a colony uses the same area repeatedly in the course of a season (Gordon 1995). When foraging trails of neighboring colonies do meet, trails do not extend past the site of the interaction. Thus the foraging trails of the five to seven nearest neighbors of a colony form a barrier which its foragers do not cross. The number of colonies within 20 m was chosen as a measure of density because colonies rarely interact with others more than 20 m away (Gordon and Kulig 1996), but when there are more than five to seven colonies within 20 m of a focal colony (Table 1), this number probably includes colonies outside its foraging range.

It is surprising that there was no effect of the number of old, large neighbors on alate production. New colonies are less likely to appear near older, larger neighbors, and colonies are more likely to interact with such neighbors, indicating that competition for foraging area is more intense with larger neighbors (Gordon and Kulig 1996). However, this effect may not be strong enough to detract from alate production.

About 20% of the colonies we observed produced no alates at all (Fig. 1). Most of these were located in extremely crowded neighborhoods. These colonies appear small for their age, in terms of nest mound size and numbers of active foragers (personal observation). Perhaps intense competition with neighbors for food has prevented them from growing large enough to obtain the resources necessary to produce alates. It seems unlikely that these colonies were too young to reproduce. Of the 9 colonies that produced no alates, 3 were 5, 1 was 6, and 5 were 7 years old, so the youngest, 5-year-old colonies were not strongly represented. Colonies younger than 5 years sometimes reproduce; previous work showed that of 77 colonies of known age that produced alates, 18% were less than 5 years old (Gordon 1995).

Because male and female alates differ in weight, the colony's investment in reproduction probably depends on the sex ratio of the alates it produces. However, we found that while alate number is related to density, there was no relationship between the sex ratio, measured as the proportion of alates that were female, and density. While the sex ratio may be affected by environmental conditions in *P. barbatus* as it is in other ant species (Nonacs 1986), we found no evidence that investment in females is influenced by density.

Since a colony reproduces for about 10 years, lifetime reproductive success probably depends mostly on factors that influence alate production in a consistent way, year after year. Local density is such a factor because colonies live for 15–20 years and rarely relocate their nests (Gordon 1991, 1992b); neighborhood density conditions tend to persist for many years.

Neighborhood density is clearly not the only factor influencing alate production. Another important, long-term factor may be variation among colonies in foraging intensity. No colony forages every day, and colony-specific differences in the number of foraging days per season persist from one year to the next (Gordon 1991). Colonies that forage more often may be able to produce more alates.

Shorter-term environmental factors may also be important. These include conditions that affect brood development such as the thermal properties of the microtopography around the nest, and the incidence of flooding. Local food supply may vary from one colony to another. However, such effects seem to be ephemeral. *P.barbatus* foragers at this study site collect seeds produced months before and dispersed by wind and rain (Gordon 1993). Seeds of different types appear to be distributed in a patchwork of regions, lasting only for several days, occurring on the scale of the distance between nests (average about 8 m) (Gordon 1993). The timing of the availability of particular seed types may affect alate production in a given year, but the spatial distribution of seeds is unlikely to persist from year to year.

The numbers of alates we counted are similar to those we estimated from Munger (1992) for *P. desertorum* and to those of Ryti and Case (1988b) for *Messor pergandei,* but are lower than counts made for *P. rugosus,* a species with colony sizes similar to those of *P. barbatus* (MacKay 1981). The disparities may reflect genuine differences among species, differences in methods of counting and the season in which alates were counted, or differences among populations in density (Gordon 1991).

It is not known how an increment in alate production translates into an increment in reproductive success. Alates from different colonies may vary in their ability to survive the mating flight and period of nest founding, and in their ability to produce the first brood. Such variation may depend on behavior, such as the speed with which a newly mated queen can dig a hole that provides refuge from predators. The variation may depend on physical condition, such as a queen's fat or water reserves; this is related to brood production in other ant species (Tschinkel 1993). Further work is needed to investigate these possibilities in *P. barbatus.* Even assuming that all alates are potentially equivalent in their ability to contribute to the founding of a colony, the relationship between alate number and reproductive success could be frequency dependent (Boomsma and Grafen 1990) and, if so, might vary from year to year with fluctuations in sex ratio and the overall number of alates on the site. Work is in progress to estimate how the alates of a particular colony contribute to the pool of reproductives that mate and settle on the site.

If alate production is correlated with reproductive success, our results suggest there may be considerable selective pressure on territorial behavior. Colonies in crowded neighborhoods can maintain alate production only by behaving in ways that allow them to obtain sufficient food despite intense competition from their neighbors.

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