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FOUNDING, FORAGING, AND FIGHTING: COLONY SIZE AND THE SPATIAL DISTRIBUTION OF HARVESTER ANT NESTS[1]

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Abstract. This study examines how the spatial distribution of nests is related to the behavioral interactions of conspecific neighbors in a population of the seed-eating ant, *Pogonomyrmex barbatus*. Colonies live for 15–20 yr, reaching reproductive age and a stable size at ≈5 yr. Spatial distributions were measured for 6 yr (1988–1993) in a population of ≈250 colonies of known age. The probability that a 1-yr-old colony occurs in a given location is related to the distance to, and ages of, its five nearest conspecific neighbors. One-year-old colonies are most likely to occur near small, 2- and 3-yr-old colonies.

Neighboring colonies encounter each other when foragers of both colonies search the same area on the same day. The probability of an encounter between two colonies decreases with the distance between their nests. For colonies of all ages, encounters are most likely with their larger neighbors, ≥5 yr old. Encounters are more likely if there was an encounter the previous day, and this effect can overwhelm the effect of distance. Two-yr-old colonies are more likely than colonies of other ages to lose ground in repeated encounters with a particular neighbor.

Though encounters are frequent, their costs are low: few of the foragers on a trail that meets a neighbor's actually encounter an ant of the neighboring colony, and interaction with a neighboring colony does not increase the typical duration of a foraging trip. If foragers of two colonies do meet, most fights are brief, with few resulting in injury or death. These results suggest that the cost of conspecific neighbors searching the same ground for seeds may be greater than the cost of behavioral interaction itself. Exploitative competition may have more important effects than interference competition on founding colony survival and thus on the spatial distribution of nests.

Key words: ants; colony size; competition for space; foraging; population, age/size-structured; spatial distributions; territorial behavior.

INTRODUCTION

Populations are made up of individuals, and the behavior and resource use of individuals generate the ecology of populations. But we rarely have the data available to link the individual and population levels. This is true of studies of competition for space. Theory shows how the details of interactions at the individual level could generate the spatial pattern of a population (Lomnicki 1980, Slatkin and Anderson 1984, Roughgarden et al. 1985, Durrett and Levin 1994). But it is often difficult to trace the relation between interactions among individuals and population-level spatial distributions.

Resource use varies during the lifetime of an individual (Werner and Gilliam 1984, Werner and Caswell 1977, Sullivan 1988), so that the age/size structure of a population strongly influences the effect of competition on population dynamics (May et al. 1974, Ebenman 1987, Nisbet and Onyiah 1994). There are few ecological studies of competition for space in age/size-structured animal populations (Ellison and Harvell 1989), but such studies of plants (Pacala and Silander 1985, Kenkel 1988) show that age/size structure can influence spatial distributions.

Competition among individuals for space, and territorial behavior, vary during the lifetime of an individual (Michener 1981, Doncaster and Macdonald 1991). When juveniles and adults have different stakes in territory acquisition, as they do in birds (e.g., Stacey and Ligon 1987) and in anole lizards (Stamps and Eason 1989), a population's age structure may determine how space is partitioned.

Here we first consider the spatial distribution of a population of one species of seed-eating ants, and test whether neighbor age/size influences the probability that a new colony has become established. Next we consider behavioral interactions of neighboring colonies within a population, and test how neighbor age/size, distance between neighboring nests, and events on previous days all influence the probability of interaction. Finally, we consider whether behavioral interactions might influence the spatial distribution of new colonies, by examining the costs of interaction for ants within colonies.

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TABLE 1. Demography of *P. barbatus* colonies at the study site.

Year	Died in preceding year	1 yr old	New, older than 1 yr	Total number of colonies	Area of study site (ha)
1988	0	29	0	155	7.6
1989	0	42	15	212	7.9
1990	2	21	22	253	9.6
1991	19	30	47	311	10.5
1992	12 (+6)	25	9	327	10.5
1993	15	42	11	365	10.5

Notes: Shown are numbers of colonies that died in the preceding year; newly founded 1-yr-old colonies; colonies new to the study site but older than 1 yr (most of these probably moved in from outside the study site, and one colony was included when boundaries were extended in 1990); and area of study site. Six colonies were excavated and removed from the study site in 1992.

SPATIAL DISTRIBUTION OF NESTS: EFFECT OF NEIGHBOR AGE/SIZE ON FOUNDING COLONY SURVIVAL

Harvester ant demography and spatial distributions

The study was performed at a site near Rodeo, New Mexico (elevation ≈1200 m), where all colonies of the seed-harvesting ant *Pogonomyrmex barbatus* have been censused, individually labelled, and mapped every summer since 1985 (techniques described by Gordon 1987, 1991, 1992*a*). Using the census data, the ages of all colonies founded since 1985 can be established. A minimum age is estimated for colonies assumed on the basis of colony size to have been 5 yr or older when the census began in 1985. Table 1 summarizes the demography of colonies at the study site.

P. barbatus compete for food with a guild of other granivorous species (Brown and Davidson 1977, Davidson 1977, 1985), including other ants, rodents, and birds. There are several other *Pogonomyrmex* species at the site (*P. maricopa, P. desertorum,* and *Ephebomyrmex imberbiculus*); all are much smaller ants with much smaller colonies (Gordon 1984) that move from year to year (D. M. Gordon, *personal observation*). At this site, interspecific competition with *P. barbatus* appears to be most intense with another seed-eating ant, *Aphaenogaster cockerelli* (Whitford and Ettershank 1975), which interferes with the foraging activities of neighboring *P. barbatus* colonies (Gordon 1988), but moves its nests frequently from year to year (D. M. Gordon, *personal observation*).

The foraging behavior of *P. barbatus* indicates there is intraspecific competition for foraging area. Bait experiments show that a colony's use of foraging space is influenced by encounters with foragers from neighboring colonies (Gordon 1991). Such encounters occur when foragers from both colonies search the same area for seeds on the same day. The site of an encounter is always the endpoint of both colonies' foraging trails. Enclosure experiments indicate colonies compete for foraging space: when a colony is prevented from encountering its neighbors, the neighbors move into its foraging area; when encounters are resumed, the colony regains some or all of its former foraging area (Gordon 1992*a*).

A *P. barbatus* colony lives to be 15–20 yr old (Gordon 1991). Every summer, after the rains have begun, winged males and virgin queens fly from their nests and form a mating aggregation. After mating, males die. Newly mated queens fly away, drop their wings, dig a new nest, and found a new colony. Since newly mated queens appear to fly away from the mating aggregation at random, there is no evidence that neighboring colonies are related. All of the ants in a colony are the offspring of a single founding queen, who continues to produce worker ants throughout her life using the sperm from her original mating flight. A colony dies when its queen dies and all of its workers, who live about a year (Gordon and Hölldobler 1988), have died. Colonies do not adopt new queens.

Colony age is related to colony size. Numbers of ants increase for the first 5 yr, reaching ≈3000 workers at age 2 yr and ≈4000 to 8000 at age 3–4 yr (Gordon 1992*a*); at about age 5 yr, colonies begin to reproduce by sending out sexual forms to the yearly mating flight (Gordon 1995). Mature colonies ≥5 yr old seem to maintain a stable size of ≈10 000–12 000 workers (MacKay 1981). Colony age is used here as a correlate of colony size, because it is possible to measure age nondestructively by a yearly census. Accurate counts of number of ants require a full excavation that destroys the colony. Colony size and growth rate probably influence resource use and spatial distribution of nests more than does age per se (Kirkpatrick 1984, Sauer and Slade 1987), so results are interpreted in terms of colony size.

Mortality of *P. barbatus* colonies seems greatest at the founding stage. Large numbers of newly mated queens are eaten by lizards and birds (D. M. Gordon, *personal observation*). Observations suggest aggregations on this site attract reproductives from an area about twice as large as the study site. It is not known how far the newly mated queens disperse after mating. Each mature colony may produce ≈30 virgin queens a year (Gordon and Wagner 1996). If 200–400 colonies of reproductive age send 10 000 queens to the mating aggregation, and if 5000 of them disperse back onto the site after mating, then the 20–30 1-yr-old colonies found on the site each year (Table 1) imply a mortality rate of ≈99%. Similar mortality rates of newly mated queens have been observed in other harvester ant species (Pfennig 1995). After the founding stage, mortality is extremely low (see Table 1 for mortality of colonies 1 yr or older). Once a colony reaches 2 yr old, its survivorship does not vary until it is ≈15 yrs old (Gordon 1991).

The density of *P. barbatus* colonies is relatively high at the site studied here (reviewed in Gordon 1991);

similar high densities have been reported elsewhere for this species (Whiting et al. 1993). Each year, ≈10% of *P. barbatus* colonies 2 yr or older relocate their nests, though nest relocation has no significant effect on nearest-neighbor distances (Gordon 1992*b*). The same colonies tend to move their nests year after year, perhaps to escape some infestation.

Here we first examine the effect of the age/size of conspecific neighbors on the location of 1-yr-old *P. barbatus* colonies, using the data from 1988–1993. Mating flights occur in the summer, and the census is made each summer, so colonies are first included in the census the summer after they were founded, at the age of 1 yr. The probability that a 1-yr-old colony occurs at a particular location thus reflects the probability that a newly founded colony can survive to 1 yr in that location.

Neighbors may influence a colony's survival to 1 yr during most of the 1st yr of a colony's life. Interaction between colonies occurs only when ants are active above ground; colonies are not in contact underground. A founding queen digs a nest within a day of mating, and never emerges from it. After a few days, there is no trace of the nest entrance. *Pogonomyrmex barbatus* workers attack founding queens that happen to wander by while searching for a nest site, but no brood raiding, or attacks on queens already in nests, has been observed. (There is one report of brood raiding by *P. rugosus* on *P. barbatus* [Hölldobler and Markl 1989] but there are no *P. rugosus* at this site.) In the laboratory, four to five nanitic workers appear after ≈2 mo; a few were observed in the field in early October, ≈10 wk after the mating flight, foraging up to 1 m from their nest. Ants rarely emerge from the nest from about November to March, so a newly founded colony may encounter neighbors when its first foragers emerge briefly in October–November, but most encounters will be in the following spring and summer, when the colony is 1 yr old.

Methods

The data consisted of the locations and ages of all colonies in the study site for 6 yr, 1988–1993 (Table 1). Fig. 1 shows the spatial distributions of nests for these years.

Measurements of nest locations were made with a compass and tape measure. A subsequent check with a Wild infrared theodolite (Heerbrugg, Switzerland) confirmed that ≈80% were accurate to within 1 m, and an additional 15% were that accurate relative to their neighbors, though less accurate relative to the 0,0 point of the coordinate system of the map.

Effects of neighbor age on the location of 1-yr-olds were tested using a proportional hazards regression (Kalbfleisch and Prentice 1980). The marginal likelihood that a 1-yr-old appears in a given location was approximated by:

$$L = \prod_{i=1}^{k} \frac{\exp(S_i\beta)}{\left[\sum_{l\in R_i} \exp(X_l\beta)\right]^{d_i}}$$

where i is the year (1988–1993). S_i is the sum of the explanatory variable vectors for 1-yr-old colonies in year i. Explanatory variables (X_i) tested were: distance to the fifth nearest neighbor (a measure of crowding), the number of the five nearest neighbors that were age 2, the number that were age 3, and so on for ages 4, 5, and 6 or older. R_i is the universe of possible locations for 1-yr-old colonies in year i (the risk set in survival analysis), and d_i is the number of 1-yr-old colonies in year i. The magnitude of the coefficient β for each explanatory variable indicates how well the variable predicts the probability of finding a 1-yr-old in location i. For each unit increase in the value of an explanatory variable, the probability changes by a factor of $\exp(\beta)$. The problem reduces to maximizing L with respect to β, achieved using a Newton-Raphson iterative technique (Miller 1981*a*).

We chose distance to the fifth nearest neighbor as a measure of crowding to stay well within the spatial range where interaction between neighbors was likely to occur. In observations of 34 colonies over 17 d (described in *Encounters between neighboring colonies*), about half the colonies met their fifth nearest neighbor (Fig. 2), and 75% of encounters between colonies were with one of the five nearest neighbors.

The universe of possible locations for new colonies was approximated as a grid of points separated by 7.5 m, which gave a total of ≈1250 possible locations (see Table 1 for actual numbers of colonies). To reduce edge effects, borders composed of straight lines were placed on the map inside the area censused (Fig. 1). Boundaries were assigned by eye; we attempted to exclude possible locations that would lack neighbors along one edge, and to include only locations that would be as closely surrounded by neighbors as other nearby colonies. All grid points and 1-yr-old colonies within these borders were included in the analysis.

The statistical significance of results was determined using Wald-type and likelihood ratio tests (Miller 1981*a*). Explanatory variables included in a combined model were chosen by first regressing each variable individually. Inspection of the results indicated that, among the nearest five neighbors, the numbers of 2-yr-olds and the numbers of 3-yr-olds were positively correlated, and the numbers of 4- and 5-yr-old, and older colonies were negatively correlated, with the location of new colonies. Therefore the numbers of 2- and 3-yr-olds were added to obtain a single explanatory variable, which showed greater statistical significance than either variable separately. The number of colonies 4 yr or older within the nearest five provides no additional information to the numbers of 2- and 3-yr-olds (since they sum to five) and was thus removed from the final model.

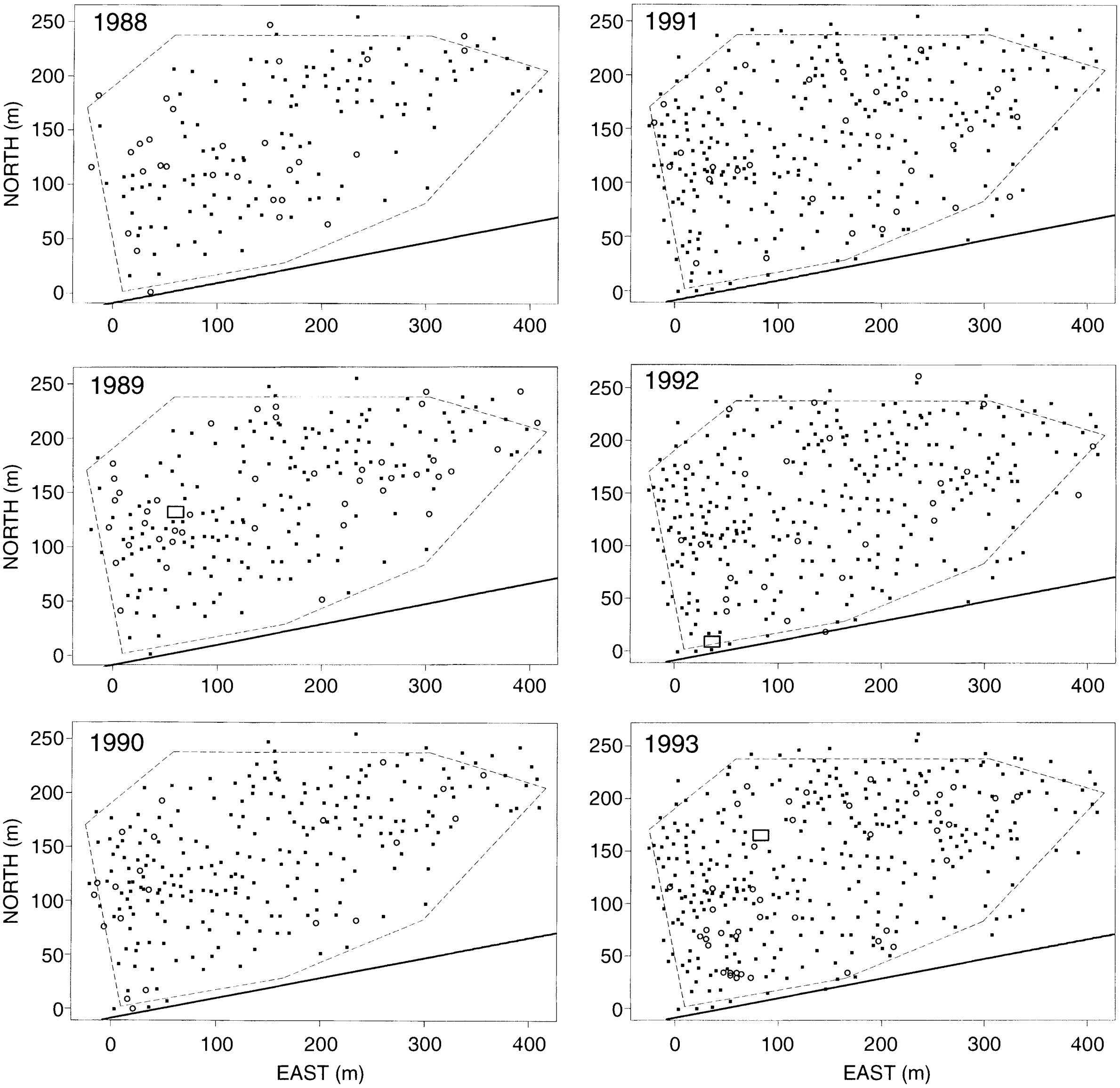

FIG. 1. Spatial distribution of *P. barbatus* colonies 1988–1993. Large circles represent 1-yr-old colonies; smaller points represent older colonies. The solid diagonal line across the bottom of each map represents a road. Rectangles show the site of the mating aggregation in the previous year; these sites are not available for 1987, 1989, and 1990. The area censused extends from the colonies shown in the upper right of each map down to the road, so the area in the lower right is empty of *P. barbatus* colonies. The dotted line shows the boundaries used for statistical analysis; details in *Spatial distribution of nests: Methods.*

To test whether the independence assumptions of the model affected the validity of the results, we also calculated jackknife estimates of the standard errors of estimated coefficients (Efron and Tibshirani 1993). The grid was divided into 25 subregions, each containing the same number of grid points, using parallel lines with a northeast slope of 0.11. Jackknife estimates were obtained by deleting each of these subregions in turn, estimating regression coefficients over the remaining subregions, and then combining the 25 coefficient vectors.

Three additional analyses were performed to check the results of the regression. First, the likelihood function is an approximation that assumes that each new colony is founded in a location independent of the location of all other newly founded colonies. But we know that two colonies cannot exist in the same location. To test the validity of the approximation, we reanalysed the data twice, once using (1) a grid in which the distance between adjacent points was divided by $\sqrt{2}$, doubling the number of possible colony locations, and (2) a grid in which the distance between points

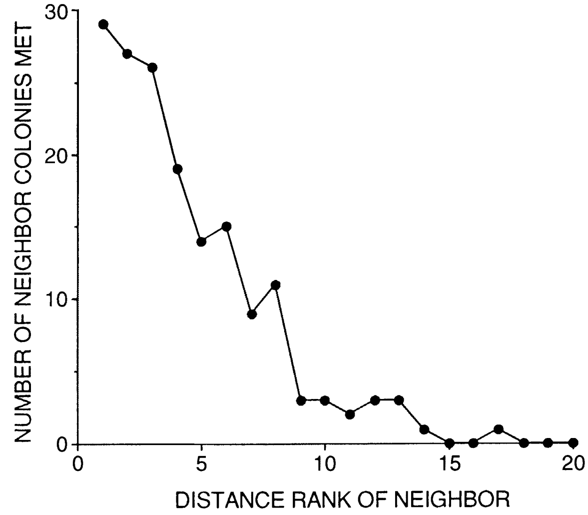

FIG. 2. Encounters as a function of neighbor distance. Shown are data from observations of 34 colonies over 17 d. The first point is the number of nearest neighbors that were encountered during the 17 d, and so on for neighbors up to the 20th nearest neighbor. Each of the 34 focal colonies has one neighbor at the indicated distance rank; thus all points are out of a possible 34.

was multiplied by $\sqrt{2}$, halving the number of possible locations. Second, the regression was performed with the restriction that possible locations of new 1-yr-old colonies were not permitted in a circle of diameter 2.33 m around each existing colony; this distance corresponds to the smallest distance ever observed between an existing colony and a new 1-yr-old. This excluded 4.6% of locations used in the main analysis. Third, to check for large-scale spatial heterogeneity in the study site, the regression was performed separately with each of two halves of the study site. The site was divided in half on a diagonal from the upper left to lower right.

Results

One-year-old colonies are more likely to appear near 2- and 3-yr-old colonies than near older ones. The combined model, incorporating both distance to the fifth nearest neighbor and the number of the five nearest neighbors that were 2 or 3 yr old, shows that both variables influence the location of 1-yr-old colonies. The likelihood-ratio test 97.5% confidence intervals verify that the two coefficients are simultaneously different from 0 at $P < 0.05$ (Miller 1981*b*) (see Table 2). The Wald-type test statistic gave similar results.

When the number of the five nearest neighbors that are 2 or 3 yr old increases by one, this increases the probability a 1-yr-old will appear by a factor ($\exp(\beta)$) of 1.35 (where β is the coefficient 0.299 corresponding to Number of 2- and 3-yr-olds within the nearest five neighbors, Table 2). One-year-old colonies are more likely to occur in crowded areas, i.e., where the distance to the fifth nearest neighbor is small (negative coefficient for Distance to fifth nearest neighbor, Table 2). For each metre that the distance to the fifth nearest neighbor is increased, the probability that a location will be the site of a 1-yr-old colony is decreased slightly, by a factor of 0.97 ($\exp(\beta)$ for the Distance coefficient -0.035).

The jackknife estimates of standard error were 0.012 for distance to the fifth nearest neighbor and 0.059 for number of five nearest neighbors of age 2 or 3 yr. These give approximately the same levels of statistical significance as the model results, indicating that different subregions of the spatial grid can be considered independent.

The further regressions performed as checks generally had results similar to the combined model. When distances between possible locations were multiplied or divided by $\sqrt{2}$, the results were virtually identical to those shown in Table 2. Thus locations of new colonies can be considered independent of each other, and apparent spatial patterns are not a consequence of the grid scale. When an area around each existing colony was excluded from the region in which a new colony could be founded, the results were the same, in magnitude and sign of coefficients and in significance levels, as for the combined model. When regressions were performed separately for two halves of the site, the results were similar for the southwest half of the study site. In the northeast half, however, results were similar for distance to the fifth nearest neighbor, but not for number of 2-yr-olds ($\beta = -0.02$, $P = 0.9$), 3-yr-olds ($\beta = -0.28$, $P = 0.06$), or 2- and 3-yr-olds combined ($\beta = 0.17$, $P = 0.2$) among the five nearest neighbors.

ENCOUNTERS BETWEEN NEIGHBORING COLONIES: EFFECT OF COLONY AGE/SIZE ON CONFLICT OVER FORAGING AREA

Harvester ant foraging behavior

The results described in *Spatial distribution of nests* show that the locations of 1-yr-old colonies are related to the age/size and proximity of their neighbors. One-year-old colonies are most likely to occur near 2- or 3-yr-old colonies, which were 1 or 2 when the 1-yr-old was founded. This section considers how encounters among foragers of neighboring colonies are related to colony age/size.

The extent to which a colony will repeat an encounter with a neighbor on subsequent days depends on colony age. Intermediate-sized colonies, aged 3–4 yr, are most likely to engage in prolonged conflicts with neighbors over foraging area, lasting for many days (Gordon 1991) and to retain area acquired while a neighbor was enclosed, even after the neighbor is released (Gordon 1992*a*). Surprisingly, the total area of a colony's foraging range is not proportional to colony size; colonies 5 yr and older do not occupy significantly larger ranges than 2-yr-olds (Gordon 1995).

When colonies meet, ants sometimes fight, seizing the legs or petiole of the opponent. Sometimes an ant

TABLE 2. Location of 1-yr-old colonies.

Independent variable	Coefficient	CI limits
Distance to fifth nearest neighbor	−0.035	−0.059, −0.016
Number of 2- and 3-yr-old neighbors	0.299	0.154, 0.442

Notes: Results are shown of a proportional hazards regression that tested how the location of 1-yr-old colonies depends on the distance to the fifth nearest neighbor, and on the number of neighbors of a given age within the nearest five neighbors. Shown are estimated coefficients and CI, the likelihood-ratio test 97.5% confidence intervals. Combined medel: likelihood-ratio test statistic = 34.27, df = 2, Max(P) = 0.0001.

manages to kill another, either by biting it into pieces or inserting its sting between sections of the other's exoskeleton. In *Cost of encounters* the duration and outcome of fighting are described in detail.

Spatial heterogeneity in food quality does not appear to influence the location of interaction between colonies. During the summer, colonies throughout the study site collect the same species of seeds, all widely distributed by wind and flooding (Gordon 1993). There are no patches that consistently provide particular seed species, even from one day to the next (Gordon 1993). Thus consistent spatial patterns of foraging, such as foraging distances, cannot be attributed to spatial patterns of food distribution.

Here we examine the factors affecting the probability of behavioral interaction among neighboring colonies.

Methods

Thirty-four colonies were observed for 17 d between 31 July and 21 August 1993, the season when foraging is at its peak (Whitford and Ettershank 1975, Whitford et al. 1976). The 34 colonies included 10 of age 2, 9 of age 3–4, and 15 of age 5 or older. In the following, the 34 colonies observed are called "focal colonies," to distinguish them from the neighboring colonies they encountered. The 34 focal colonies were chosen at a range of densities: about half the colonies of each age class had 7 or more (up to 14) neighboring colonies of *P. barbatus* within 20 m; the rest had only 2–6 conspecific neighbors within 20 m.

Every colony was observed several times on each of the 17 d. For each colony, we recorded the location of all encounters between its foragers and those of any neighboring colonies. Foragers may cover a wide area, and the confluence of foraging trails of two colonies may occupy several square meters. An encounter's location was measured (in the same coordinate system used to measure nest sites) at the center of the region occupied by foraging ants of both colonies. If the encounter spread over an area >1 m^2, multiple locations were measured, each at the center of a 1-m^2 region. These data were used in the analysis of encounter location (described below in *Location of encounters*) and encounter frequency, wherein an "encounter" is one occasion on which a focal colony met one neighbor, regardless of the number of locations measured for this pair of colonies on that day. Fig. 3 illustrates the encounters of one relatively crowded, and one less crowded, focal colony in each of the three age classes.

Probability of encounters.—A logistic regression was used to evaluate the probability that two neighboring colonies meet. For this analysis, we included all colonies with nests within 24 m of the nest of a focal colony, a criterion that included 99% of all encounters. There were 358 such colonies, of which 124 interacted with the 34 focal colonies over the 17 d. For comparison to the previous analysis, all but 1 of the 34 focal colonies had five or more conspecific neighbors within 24 m.

We modelled the probability of an encounter between a focal colony and one of its neighbors using the following variables: distance between the two colonies; age class of the focal colony (2 yr, 3–4 yr, ≥5 yr); age class of the colony encountered (1, 2, 3–4, ≥5); the day on which the encounter occurred; and whether the two colonies encountered each other on each of the previous 3 d, using one indicator variable for each of the 3 d. The latter three variables are included to capture any autoregressive time series in the data.

Logistic regression models the log of the odds ratio

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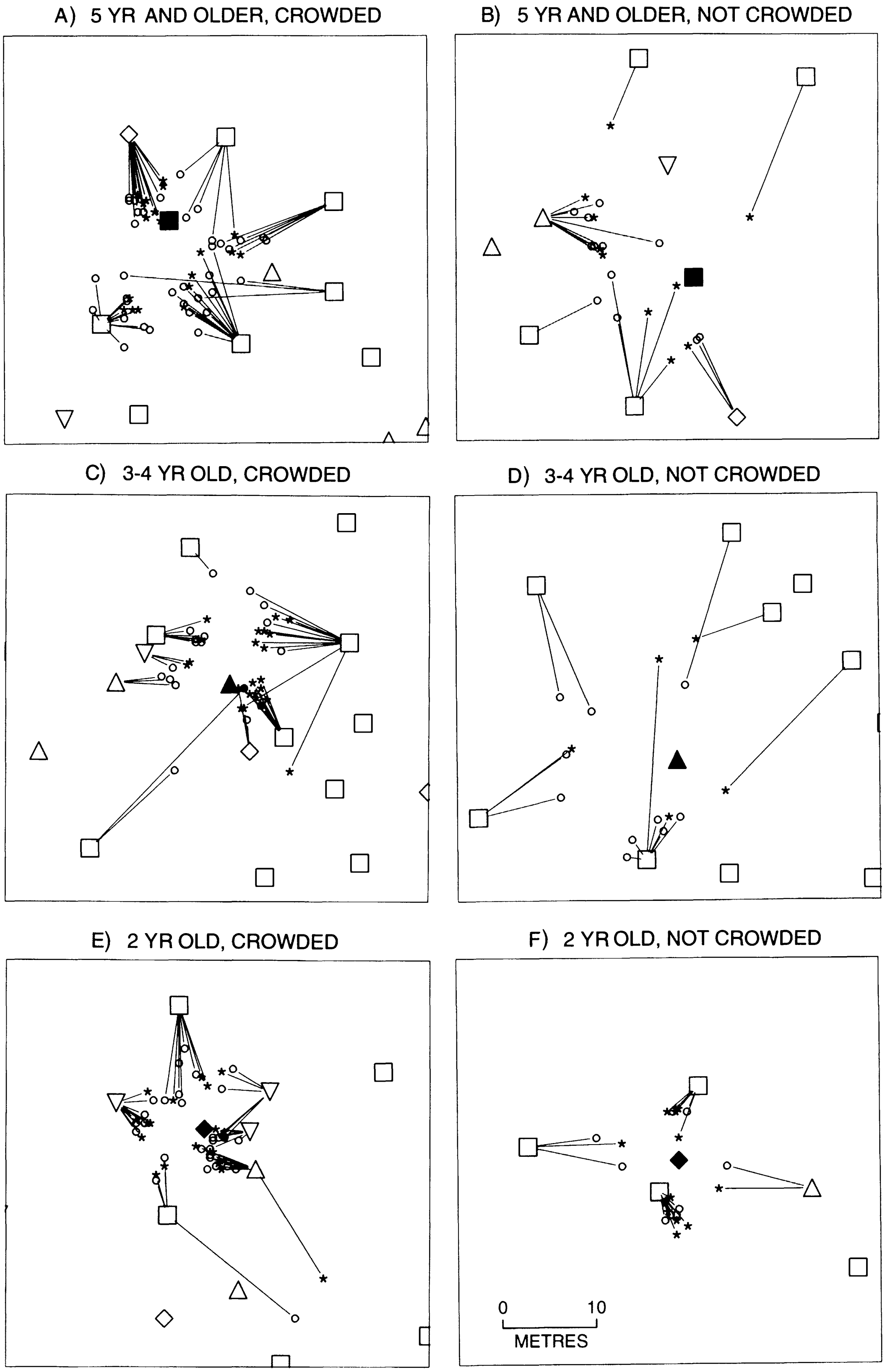
FIG. 3. Colony age/size differences in rate of encounter with neighbors. Each figure shows the location of all encounters of one focal colony during 17 d of observation. All figures are to the same scale (shown in F). Shown are the encounters of a relatively crowded, and a less crowded, 2-yr-old, 3–4-yr-old, and ≥5-yr-old focal colony. The focal colony's nest is shown with a filled symbol. Shapes represent colony age: inverted triangle, 1-yr-old; diamond, 2-yr-old; upright triangle, 3–4-yr-old; square, 5-yr-old or older. A small circle shows the site of one encounter on one day that did not result in fighting; a star shows the site of an encounter that included fighting. A line connects the encounter site to the nest of the neighbor that met the focal colony. On the day of the encounter, there was a foraging trail from the focal colony to the site of the encounter, and another from the neighbor (not necessarily along the straight line shown) to the site of the encounter; the small circle shows where these two trails overlapped.


A) 5 YR AND OLDER, CROWDED
B) 5 YR AND OLDER, NOT CROWDED
C) 3-4 YR OLD, CROWDED
D) 3-4 YR OLD, NOT CROWDED
E) 2 YR OLD, CROWDED
F) 2 YR OLD, NOT CROWDED
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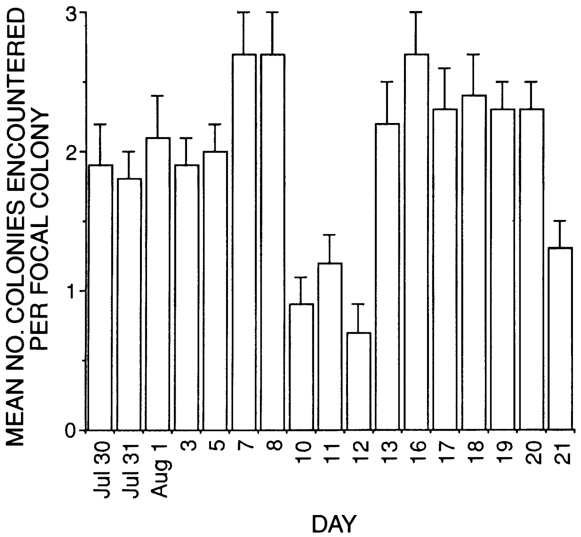

FIG. 4. Day-to-day variation in number of encounters with neighbors. Each bar shows the mean number of colonies encountered per focal colony. Bars show the standard error of the mean.

of an event as a linear function of the explanatory variables. The coefficient β associated with each variable is used to calculate the odds ratio. Here a unit increase in the value of a variable X_i changes the odds of an encounter between colonies by a factor of exp (β), the odds ratio. If β_i is positive, the odds ratio will be >1, and increasing the variable X_i increases the probability of an encounter. If β_i is negative, the odds ratio will be <1, and increasing X_i decreases the probability of an encounter.

We obtained maximum likelihood estimates of the parameters of the logistic regression. After regressing each variable individually, we chose independent variables using a stepwise selection process based on the approximate chi-square distribution of the reduction in deviance achieved by adding variables. Only interaction terms considered biologically relevant were tested for statistical significance. The analysis was performed with the statistical computer language S, using the S stepwise selection program. Based upon Hosmer and Lemeshow's (1989) test procedure, a linear measure of distance was an adequate independent variable without transformation. For age classes of the focal and encountered colonies, the class representing ages 5 and older was the baseline against which the other classes were compared. That is, for a discrete variable with n levels, only $n - 1$ coefficients were estimated, corresponding to all but the baseline level. The day effect was modelled with $n - 1$ orthogonal Helmert contrasts of the design variables for the n days (Chambers and Hastie 1992).

Data were collected on 17 d within a 23-d period (see Fig. 4). When testing the effect of an encounter the previous day, "the previous day" was taken to be the most recent previous day for which data were collected. Only the last 14 of the 17 d were used in the analysis, because for the first 3 d of observation, data were not available for the three variables representing encounters on the previous 3 d.

Some focal colonies were located within 24 m of other focal colonies, and we avoided double counting of the encounter data for these pairs. For each day, the data on encounters (encounter or no encounter) were included for only one colony of the pair, with the colony to be included chosen at random.

If one encounter reduces the probability that the same colony will have other encounters on the same day, an independence assumption of the model would be violated. To test this, a separate logistic regression was performed with "encounter with another colony on the same day" as the explanatory variable. The results showed that an encounter with a neighbor on one day is associated with a higher, not lower, probability of encounters with other neighbors on the same day (Table 3); on days when colonies encounter their neighbors, they are likely to encounter more than one. This may be due to an effect of temperature or other weather conditions on the general activity level of all colonies. The day effect was included in the larger model to take this result into account.

As a further check of the independence assumptions, we obtained nonparametric jackknife estimates of the standard error of included variables (Efron and Tibshirani 1993). These estimates were calculated by removing the modelled data for each focal colony separately, re-estimating coefficients, and combining the separate estimated coefficients to estimate standard errors. The final, combined model includes all explanatory variables and selected two-way interactions (initially chosen by the stepwise selection process described above) for which model-produced and jackknife-estimated P values were both <0.05.

We incorporated the effects of time in the logistic regression by modelling the data as a pth order Markov model, with probability of an encounter, conditioned on the last p days' events, independent of events prior to p days ago. We examined time series trends in the data by calculating the average lagged correlations, averaged over 358 colony pairs that interacted, and lagged from 1 to 16 d. We found that 3 d was the value of p that best explains the time series trend in the data, by including terms up to 5 d in the regression and eliminating those that were not statistically significant. To confirm that the assumption of conditional independence was satisfied by the three-order Markov model, we estimated time series trends left unexplained by the model by calculating average lagged correlations for Pearson residuals from the model (McCullagh and Nelder 1989).

To assess the goodness of fit of the combined model, we used a test statistic C, which has approximately a

TABLE 3. Probability of encounter between neighboring colonies.

Variable	Odds ratio	Coefficient	Standard error of coefficient	Jackknife standard error
Day (overall $P < 0.001$)				
Distance	0.16	−0.18	0.015	0.025
Encounter on previous day	0.99	−0.01	0.339	0.397
Encounter 2 d ago	3.07	1.12	0.134	0.187
Encounter 3 d ago	2.18	0.78	0.138	0.163
Age of colony met compared to ≥5 yr old):				
1 yr	0.38	−0.98	0.227	0.271
2 yr	0.59	−0.53	0.318	0.405
3–4 yr	0.50	−0.69	0.198	0.241
Age of focal colony (compared to ≥5 yr old):				
2 yr	0.94	−0.06	0.132	0.202
3–4 yr	0.69	−0.38	0.130	0.172
Distance × Encounter on previous day	4.21	0.14	0.020	0.030
Age of colony met × Encounter on previous day				
1 yr	3.03	1.11	0.357	0.333
2 yr	1.48	0.40	0.508	0.438
3–4 yr	2.59	0.95	0.299	0.338

Notes: Shown is the final model, which includes only terms significant at $P < 0.05$. Only the overall P value is listed for the day effect: see *Encounters between neighboring colonies . . . Methods: Probability of encounters* for further details.

chi-square distribution; a high P value indicates the model fits the data (Hosmer and Lemeshow 1989).

Probability of fighting.—Logistic regression was used, as in the analysis of the probability of encounters, to evaluate the probability that fighting occurs when two neighboring colonies meet. Data included only the 1090 encounters that occurred during the 17 d of observation (excluding as before the initial days for which data on previous days were not available). We modelled the probability of fighting contingent on the occurrence of an encounter. Explanatory variables were: distance between the two colonies; age class of the focal colony; age class of the colony encountered; day of encounter; whether the colonies met and fought on the previous day; and whether they met and fought 2 d previously. All aspects of the rest of the analysis were similar to those for probability of encounters. Effects of time were incorporated as before; the highest number of previous days found to be statistically significant was one.

Location of encounters.—Several analyses were performed to examine the effect of neighbor location, and neighbor age, on the location (rather than the probability of occurrence) of encounters between colonies. Focal colonies were classified as "crowded" or "not crowded," depending on whether the fifth nearest neighbor was within 17.5 m. This criterion divided the focal colonies of each age class approximately in half; thus "crowded" is used here to mean a density greater than the median local density of *P. barbatus* colonies; "not crowded" means a density lower than the median.

The first step was to examine the dispersion in space of a series of encounters between two colonies. In this and subsequent analyses described in this section, data were included only for those pairs of colonies that met at least twice in the 17 d of observation. For each pair of colonies we found those two encounters that were most distant from each other. To normalize for distance between colonies, this maximum distance between encounters was divided by the distance between the nests of the two colonies. The scaled maximum distance between encounters was used as the variate in an ANOVA with factors of crowding (crowded or not crowded), focal colony age class (2, 3–4, or ≥5 yr), age class of colony met (1, 2, 3–4 and ≥5 yr), total number of encounters between the two colonies in the course of the 17 d of observation (grouped as 2–5, 6–9, 10–13, or 14–17 encounters), and the interaction of focal colony age class and age class of colony met. Because there was a significant effect of number of encounters grouped, a regression was performed on scaled maximum distance between encounters vs. total number of encounters as a continuous variable.

The next two sets of tests examined whether one colony could be said to "win" a series of encounters by gaining ground from the other. First, we examined the spread between the first and last encounters observed during the 17 d of observation. This distance between first and last encounters was divided by the distance between the nests of the two colonies, and used as the variate in an ANOVA with the same factors as the test described in the previous paragraph.

Next, we calculated an index of the amount of ground gained over the 17 d of observation by finding, for the first and last encounters observed between each pair of colonies, the distances from the nest of the focal colony (df_1 for the first encounter and df_2 for the last encounter) and the distances from the nest of the colony it met

TABLE 4. Probability of fighting between neighboring colonies.

Variable	Odds ratio	Coefficient	Standard error of coefficient	Jackknife standard error
Day (overall $P < 0.001$)				
Fighting on previous day	1.41	0.35	0.154	0.160
Distance	0.65	−0.04	0.015	0.015
Age of colony met (compared to ≥5 yr old):				
1 yr	0.40	−0.91	0.249	0.263
2 yr	0.78	−0.25	0.347	0.325
3–4 yr	0.62	−0.48	0.183	0.155

Notes: Shown is the final model, which includes only terms significant at $P < 0.05$. Only the overall P value is listed for the day effect; see *Encounters between neighboring colonies . . .: Results: Probability of encounters* for further details.

(de_1 and de_2). The index of amount of ground gained was $(df_2/de_2)/(df_1/de_1)$. This index increases as more ground is gained by the focal colony, i.e., as the last encounter gets further from the focal colony than the first one. This index was used as the variate in an ANOVA with the same factors as above.

Results

Probability of encounters.—The probability that two colonies will meet on any given day depends on the distance between their nests, their ages, the day, and whether they met on the three previous days. Each of these variables, considered separately, had a significant effect (Table 3). Fig. 3 illustrates the effects of distance and colony age.

There were 358 colonies within 24 m of the focal colonies, each contributing 17 possible days on which an encounter could occur, and 1077 encounters occurred involving these 358 colonies. Thus the overall probability of an encounter between any 2 colonies within 24 m of each other is 0.18 ($=1077/(17 \times 358)$).

The probability of an encounter between two colonies decreases with the distance between their nests; an increase of 10 m decreases the probability of an encounter by a factor of 0.16 (odds ratio for Distance, Table 3). In Tables 3 and 4, odds ratios involving distance are shown with respect to a change in distance of 10 m.

Colony age has a strong effect on the probability of encounter. Focal colonies in all age classes were more likely to encounter colonies of age 5 yr and older than to encounter any younger ones. The probabilities that any colony (focal colonies were aged 2 or older) will meet a colony 1, 2, and 3–4 yr old are all lower than the probability it will meet a colony of age 5 yr or more, by the factors 0.38, 0.59, and 0.50, respectively. The age class of the focal colony also influenced the probability of an encounter (Fig. 3). Compared to colonies 5 yr and older, 2-yr-old colonies are slightly (but not significantly) less likely (odds ratio 0.94) and 3–4 yr-old focal colonies significantly less likely (odds ratio 0.69) to encounter their neighbors.

An encounter on previous days increases the probability of future encounters. If two colonies met 2 or 3 d previously, whatever their ages, the probability they meet today is increased (odds ratio 3.07 for 2 d, 2.18 for 3 d previously).

The effect of colony age on the probability of an encounter (i.e., encounters are less likely with younger colonies) is mediated by the effect of an encounter the day before. If a focal colony met another colony of any age on the previous day, the probability of an encounter is increased, so that it becomes the same as that of meeting a 5-yr-old colony. The odds ratios for meeting a 1, 2, and 3–4 yr old colony that was met the day before are 1.14, 0.87, and 1.30, respectively (for each age class, this is the odds ratio for Age of colony met times the odds ratio for the interaction of Age of colony met × Encounter on previous day). To check whether these odds ratios indicate a statistically significant difference from the probability of meeting a 5-yr-old colony, we calculated 95% confidence intervals. There was no significant difference; confidence intervals for each odds ratio contain one.

The effect of an encounter the previous day interacts with the effect of distance. If two colonies met on the previous day, then the probability of an encounter decreases with 10 m of internest distance by a factor of 0.67 (4.21, the odds ratio for the interaction of Distance × Encounter on previous day, times 0.16 for each 10 m of internest distance; see Table 3). Thus an encounter the previous day reduces the effect of distance, from a factor of 0.16 to one of 0.67.

There is considerable day-to-day variation in the probability of encounters between colonies. On some days, encounters are much more likely than others. Overall, the day effect was significant ($P < 0.0001$), with some of the statistically significant coefficients negative and some positive; odds ratios varied from 0.21 (10 August) to 3.2 (16 August). Fig. 4 shows the number of encounters on each day that colonies were observed. This is consistent with the result of the separate logistic regression showing that an encounter with one neighbor increases the probability of meeting other neighbors the same day by a factor of 1.90 (Table 3);

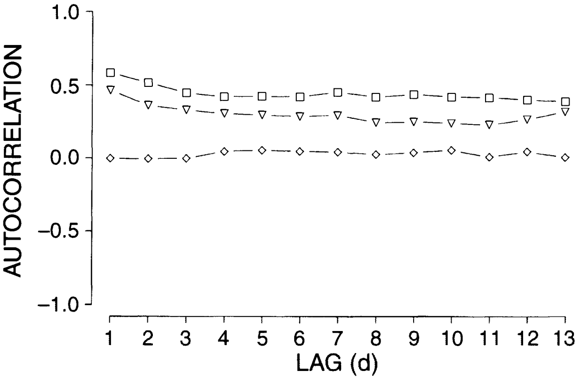

FIG. 5. Temporal autocorrelation of probability of encounter. The three lines show the extent to which the combined model of the logistic regression captures the time series trend in the data. Average lagged correlations for: (open squares) the time series of encounters between each of the 358 colony pairs that met, (open triangles) Pearson residuals for the logistic regression model of probability of encounter with no time series component included, and (open diamonds) Pearson residuals for the combined model including the effect of three previous days on probability of encounter.

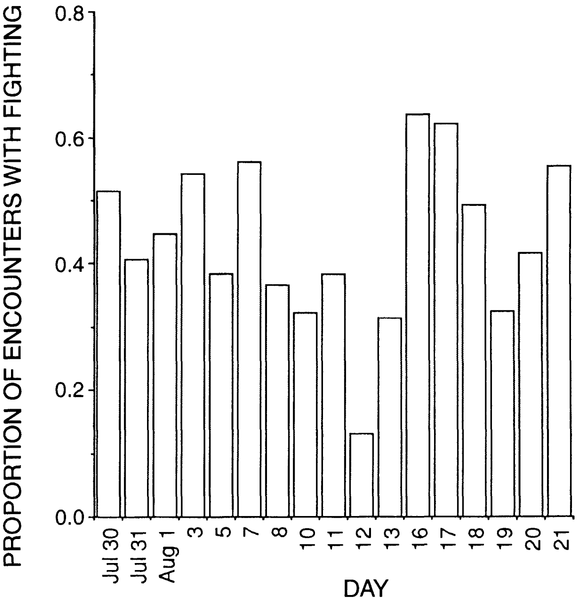

FIG. 6. Day-to-day variation in proportion of encounters that include fighting. Each bar shows the proportion of encounters that included fighting, out of the total number of encounters that the 34 focal colonies had on the indicated day.

on days when encounters are likely, colonies tend to encounter many neighbors simultaneously.

The tests of independence assumptions indicate the results of the model are valid. Jackknife standard errors did not differ much from those of the model (Table 3). The assumption of conditional independence (i.e., the probability of encounter, conditioned on the previous three days' events, is independent of events prior to 3 d ago) is supported by examining the temporal correlations before and after fitting the combined model (Fig. 5). It appears that serial correlation is effectively removed in the model because the average lagged correlations of the Pearson residuals, which characterize the temporal trends left unexplained by the model, show negligible temporal autocorrelation. The test statistic C ($C = 12.58$, df = 8, $P = 0.13$) indicates an acceptable fit for the combined model; this model, which represents the null hypothesis, cannot be rejected.

Probability of fighting.—The more distant two colonies' nests are, the less likely are the colonies to fight, by a factor of 0.65 per 10 m of internest distance (Table 4). Fighting the previous day increases the likelihood that two colonies will fight, by a factor of 1.41 (Table 4). Focal colonies were less likely to fight with colonies aged 1, 2, or 3–4 yr than with colonies 5 yr old or more (odds ratios are 0.40, 0.78, 0.62, respectively) (Table 4; see Fig. 3).

On some days, most encounters lead to fights. On other days, colonies meet but do not fight. Overall, the day effect was significant ($P < 0.0001$), with odds ratios ranging from 0.22 (12 August) to 2.30 (16 August). Fig. 6 shows the proportion of encounters in which fighting was observed; on average, fighting occurred in 44% of encounters.

The probability that two colonies will fight on any given day depends on whether they fought the day before, but not on whether they fought 2 d before (Table 4). Thus the probability of fighting today, conditioned on whether fighting occurred yesterday, can be considered independent of prior fighting events. This confirms one independence assumption of the logistic regression. Jackknife estimates of standard errors of the coefficients were similar to the model standard errors, further corroborating the independence assumptions of the model. The test statistic C ($C = 6.34$, df = 8, $P = 0.61$) indicates a good fit for the combined model.

Location of encounters.—The more often a pair of colonies met, the more their encounters were spread out in space. Maximum distance between the sites of any two encounters observed for a given pair of colonies depended significantly on the total number of encounters they had ($F_{3, 115} = 10.2$, $P < 0.0001$). The regression of the scaled maximum distance between encounters on number of encounters had a coefficient of 0.07 ($r^2 = 0.18$, $F_{1, 136} = 30.6$, $P < 0.0001$). There were no significant effects of age of focal colony ($F_{3, 115} = 0.64$, NS) or age of colony met ($F_{4, 115} = 1.0$, NS); thus although the interaction of focal colony age × age of colony met was significant ($F_{11, 115} = 2.1$, $P < 0.03$), this interaction probably is not biologically meaningful.

The distance between the first and last encounters observed between a given pair showed no effect of crowding ($F_{1, 115} = 0.9$, NS), focal colony age ($F_{3, 115} = 1.6$, NS), age of colony met ($F_{4, 115} = 1.2$, NS), total number of encounters ($F_{3,115} = 2.0$, NS), or the focal colony age × age of colony met interaction ($F_{11,115} = 1.7$, NS).

Which colony of a pair gains ground in a series of encounters depends on the ages of the colonies involved. Focal colonies of any age were most likely to gain ground against 2-yr-olds. There was a significant effect of age of the colony met on the index of amount of ground gained over the 17 d of observation ($F_{4,115} = 3.7$, $P < 0.01$). Larger values of the index mean that the focal colony gained more ground; the last encounter was farther from the focal colony than the first one. Average values of the index, by age of the colony met, were 0.89 when 1-yr-olds were met, 4.52 for 2-yr-olds, 1.00 for 3-yr-olds, 0.88 for 4-yr-olds, and 1.56 for colonies 5 yr or older. There were no significant effects, on amount of ground gained, of crowding ($F_{1,115} = 0.1$, NS), focal colony age ($F_{3,115} = 0.7$, NS), number of encounters ($F_{3,134} = 0.8$, NS), or the focal colony age × age of colony met interaction ($F_{11,115} = 0.9$, NS).

COST OF ENCOUNTERS

Cost of conflict

The results of *Spatial distribution of nests* show that the location of a 1-yr-old colony is related to the age of its neighbors; its nearest neighbors tend to be small colonies, aged 2 or 3. The results of *Encounters between neighboring colonies* show that 1-yr-old colonies are rarely encountered by their smaller neighbors. These results, considered together, suggest that a 1-yr-old colony is most likely to occur where it is surrounded by small neighbors least likely to engage it in interactions.

How important is the cost of encounters with neighbors? Time spent interacting with a neighbor is time taken from searching for food. Ants foraging on a trail that meets a trail of a neighboring colony may have to spend more time per foraging trip. In a group of foragers that rarely return to the nest without food (Gordon 1991), the longer each foraging trip lasts, the less food obtained overall. Moreover, if fighting is often fatal, then encounters between colonies could mean a loss of workers as well as of foraging time.

Interaction between colonies could also have indirect costs. When two colonies meet, it is because they are both attempting to forage in the same place, which may result in resource competition.

Methods

Two measures of the cost of encounters between colonies were made in the summer of 1994: (1) effect of encounters on the duration of a foraging trip, and (2) cost of fighting in injury or death. Several factors might influence the duration of a foraging trip: food availability, temperature (which affects speed of forager movement; ants move faster at higher temperatures), and colony age/size (which is correlated with the distance that a colony's foragers travel). To control for these factors, the duration of foraging trips was always measured simultaneously in two colonies of the same age/size. In one of the two colonies, an encounter with a neighbor was taking place, and a forager was observed heading in a direction where its colony's trail met the trail of a neighboring colony. In the second colony, there were no encounters; none of its trails met those of any of its neighbors. Comparison of trip length on the same day should minimize variation due to day-to-day fluctuations in food availability; comparisons of colonies of the same age should minimize variation due to colony size; comparisons at the same time should minimize variation due to hour-to-hour fluctuations in weather. For each trip, we recorded the duration of the trip, from the time the ant left the nest mound until it entered the nest entrance on its return, and the duration of any interaction with ants of neighboring colonies. Interaction between ants was considered to last as long as the ants engaged in antennation, fighting, or obvious alarm behavior such as running in circles. A total of 58 pairs of foraging trips were recorded, in 14, 15, and 14 different colonies of age class 2, 3–4, or ≥5 yr, respectively, with approximately the same number of observations per colony.

Fighting was considered to have two possible costs: time spent away from foraging, and possible injury or death. We recorded the duration of fights and the incidence of injury and death. To do this, we looked for places where the foraging trails of two colonies met and fights were occurring. A fight was considered to begin when the ants' legs left the ground and they began to tumble around, and it ended either when the ants separated and moved away from each other, or when some ant(s) had died and any remaining ones moved away. A total of 133 fights were observed in 51 colonies, of which 127 involved two ants and 6 involved three or four ants.

Results

Effect of encounters on duration of foraging trips.—When the trails of two colonies meet, the duration of foraging trips on those trails does not increase. Foraging trips in colonies not engaged in any interaction took an average of 22.8 min (SD 22.9, range 4–138 min, median 17.5 min); trips in the direction of an encounter with a neighboring colony took an average of 23.4 min (SD 26.3, range 2–165 min, median 16 min), $n = 58$ for each group. There was no significant difference between the duration of foraging trips of the two groups (Wilcoxon signed-ranks test, pairing observations of two colonies of the same age observed at the same time, $z = -1.12$, $n = 58$, $P = 0.13$). There were 16 observations when the forager actually met an ant of another colony. Meeting a non-nestmate did not significantly increase the duration of these 16 foraging trips (Wilcoxon signed-ranks test, $n = 16$, $T = 38$, NS).

The duration of foraging trips was recorded in ants chosen at random as they left the nest mound. One estimate of the probability that an ant travelling on a trail that intersects a neighbor's trail will actually meet a forager of the neighboring colony, is the proportion of this random sample that did so. Of the 58 foraging trips made by ants foraging in the direction of an encounter with a neighbor, the forager actually met an ant of the other colony in only 16 cases (28%). In the 58 trips made by foragers of colonies not engaged in an encounter, none of the foragers met any ants of other colonies.

Most of a foraging trip is devoted to searching. Usually a forager appears to begin searching as soon as it leaves the nest mound. Once it finds a food item, the ant proceeds directly back to the nest. The duration of the foraging trip depends mostly on how quickly the forager finds a seed. An ant travelling in a straight line moves at a rate of ≈2–3 m/min at temperatures usual on a sunny day in midsummer for the peak of foraging activity, ≈9:30 a.m. (Gordon 1984), ≈45–50°C (Whitford et al. 1976). While foraging distances range from 1 to 20 m (Gordon 1992*a*), most are <10 m. Thus if the ant were to travel to the farthest point directly, and then return immediately, most foraging trips would last only 5 min; in fact, most last ≈23 min because of the time spent searching.

Duration and outcome of fights.—Fights do not always end in injury or death. Of the 133 fights observed, only 28, or 21%, ended in injury or death for any of the participants. Ten ended in death for both or all three of the ants involved, 17 in death for one of the ants involved, and 1 in injury for one of the ants.

Most fights that end in no injury last a very short time. Of the 105 fights that resulted in no injury or death, all but 8 lasted 1 min or less (mean duration 39.7 s, median 19 s, range 1–638 s). Fights that resulted in injury or death lasted much longer (mean duration 42 min, median 1328 s or 22 min, range 240–150 000 s). Duration of fights in the case of no injury was significantly shorter than when death or injury occurred (Kolmogorov-Smirnov, df = 2, z = 4.4, two-tailed $P < 0.0001$).

Fights that lasted longer were more likely to be observed, and long fights were more likely to end in death. Thus 21% is probably a high estimate for the number of fights that end in death. Of the 133 fights, 105 were observed from beginning to end. Of the fights not observed from the beginning, 7 ended with the ants separating, uninjured, and 21 ended in death or injury to one or more participants.

DISCUSSION

Location of newly established (1-yr-old) colonies

The probability a new 1-yr-old colony will become established at a site is related to the ages of neighboring colonies. One-year-old colonies tend to occur near other young, small colonies. A population of ant colonies could thus be compared to a forest, in which large individuals crowd out young, small ones.

Factors besides neighbor age must influence the probability that a new colony becomes established at a given site. Interspecific interactions, not considered here, may have important effects. Soil and moisture conditions influence the survival of founding colonies in other *Pogonomyrmex* species (Rissing 1988, Munger 1992) and probably do in *P. barbatus* as well. However, the results presented here do not support the hypothesis that persistent physical attributes of a location, such as soil type, are more important than the configuration of neighbors. If certain sites were advantageous year after year, then new colonies should occur year after year in the same places, which they do not (Fig. 1). A jackknife test in which the study site was divided into 25 subregions showed no discernible variation among subregions in the probability that 1-yr-old colonies would be located there, though the two halves of the study site did differ. If certain sites were consistently more advantageous for founding colonies, then in the long term, since colonies rarely relocate their nests (Gordon 1992*b*), colonies of all ages should be clustered together. Instead, the location of 1-yr-olds varies from year to year, and 1-yr-olds tend to be located away from colonies 5 yr or older.

The results confirm that distance to neighbors and neighbor age/size account for a highly significant portion of the variation in location of 1-yr-old colonies. One plausible explanation for this is the relation of neighbor size and the intensity of competition for food. The present study is the first to track spatial distributions of a population of individually labelled ant colonies over many years, but the relation of neighbor age and competition for food, suggested here, has long been suspected to occur in ant populations. Some empirical studies show that larger colonies use more resources than small ones (Brian and Elmes 1974, Tschinkel 1993), and that older colonies may reduce the survival of younger ones (Ryti and Case 1988, Wiernasz and Cole 1995); this has been incorporated into theoretical predictions of spatial distributions of ants (Levings and Traniello 1981, Ryti 1991, Ryti and Case 1992).

One-year-old colonies are slightly more likely to occur in crowded areas. This may be because founding colonies tend to cluster together, so that the following year hospitable sites with a high proportion of 2–3 yr old neighbors tend to be relatively crowded. Clustering of founding colonies could arise if queens tend to dig nests near the site of the mating aggregation (which changes from year to year; see Fig. 1). Further data are needed to test this.

Colony size and the outcome of encounters

On the day-to-day time scale, the probability of an encounter between the foragers of two colonies, and the location and outcome of that encounter, are all related to the sizes of the colonies involved. Harvester ants currently provide the textbook example of stable, nonoverlapping territories (e.g., Krebs and Davies 1984) because colonies were thought to use permanent trails that never meet (Hölldobler 1976). But the present study shows that encounters are common in *P. barbatus*: over 17 d, 34 colonies engaged in 1090 encounters with their neighbors, a rate of 1.9 encounters per colony per day.

For colonies of all ages, the probability of encounter with a neighbor decreases with distance to it. Irrespective of distance, a colony is less likely to meet a young, small neighbor than an old, large one (Fig. 3). Though total foraging area covered is similar for colonies 2 yr and older (Gordon 1995), the distance a trail can extend from the nest increases with colony size (Gordon 1992*a*). A consequence of this relation between colony size and foraging distance is that a colony is more likely to meet a large neighbor (5 yr or older) than it is to meet a smaller, younger one because the larger colony is more likely to enter any neighbor's foraging range. Like encounters in general, fighting is most likely with large colonies.

For colonies of all ages, an encounter one day is likely to be followed by an encounter the next, and fighting one day is likely to be followed by fighting the next. One consequence of repeated encounters is the increased dispersion in space of future encounters. On average, every new encounter between a pair of colonies causes the cluster of their encounters to spread by almost 10% of the distance between their nests. This suggests that both the colonies involved in an encounter respond by foraging elsewhere. However, the trails of two neighboring colonies are likely to reach overlapping areas, so encounters tend to be repeated day after day in different places.

The extent to which colonies can avoid encounters depends on colony age and size. Age differences in day-to-day effects can overwhelm the effect of distance (see Fig. 3). A small colony is less likely than a large one to meet a neighbor, but the day after an encounter with a neighbor, a small and a large colony are equally likely to meet the neighbor again. Intermediate, 3–4-yr-old colonies are most likely to repeat encounters (odds ratio of 1.30 for Age of colony met × Encounter on previous day interaction); this result for undisturbed colonies is consistent with the results of previous manipulative experiments (Gordon 1991, 1992*a*).

The losers in this continuous, day-to-day adjustment of foraging areas seem to be the smaller colonies. Focal colonies of any age were much more likely to gain ground against 2-yr-old neighbors in the course of repeated encounters, than against neighbors of any other age. The index of foraging area gained from 2-yr-old colonies by their neighbors was about four times as high as that for other ages.

When two colonies interact on one day, the probability that they will meet the next day is increased. If they fight on one day, then if they meet the next day, the probability they will fight again is increased. This suggests that colonies should descend into a maelstrom of perpetual fighting. What seems to prevent this is that on some days, ants are unlikely to fight. For example, Fig. 6 shows that on 12 August, the proportion of encounters in which fighting occurred was low. Perhaps fighting is induced by a chemical cue that is more concentrated in some weather conditions.

TABLE 5. Estimate of yearly losses due to fighting with neighbors.

Colony age	Total foragers (TF)	Trails per colony (t)	Foragers per trail (TF/t)	Ants per trail-day lost in fights (TF/t × d)	Ants per year lost in fights (TF/t × d × FD × E)
≥5	3780	4	945	2.5	990
3–4	2604	4	651	1.7	681
2	967	3	322	0.8	337
1	432	3	144	0.4	151

Notes: Yearly losses are calculated by assuming 1.9 encounters per day (E), probability of death per encounter (d) of 0.002625, and 210 foraging days per year (FD). Number of trails per day per colony (t) is an average based on maps of the foraging areas of colonies of known age (Gordon 1991, 1995). See *Discussion* for explanation of estimates of other variables.

Do behavioral interactions between colonies influence spatial distribution of nests?

The effect of neighbor age/size on founding colony survival, and the effects of age/size on day-to-day encounters between neighbors, seem to be mutually consistent. One-year-old colonies tend to occur near 2- or 3-yr-olds. Foragers of a newly founded colony are least likely to meet those of young, small neighbors. Does interaction with neighbors itself decrease a founding colony's chances of survival to be 1 yr old?

The cost of an encounter between neighboring colonies is surprisingly low. Encounters have no significant effect on the duration of foraging trips. Losses due to fighting are also low. Fighting is usually brief, ending in injury or death in only 21% of fights.

One way to assess the consequences of encounters for colony survival is to estimate the numbers of ants lost each year to fighting (Table 5). This is (number of foraging days per year) × (probability of encounter per day) × (ants lost per encounter). Maximum number of foraging days per year is estimated as 210 d (1 April–30 October) (Whitford et al. 1976, MacKay 1981 for *P. rugosus*, a species with similar ecology), though most colonies are not active every day of the foraging season (Gordon 1991). The average frequency of encounter per colony per day is the total number of encounters observed per colony-day, 1077/(34)(17) = 1.9. Since each encounter involves one foraging trail, 1.9 is also the average number of trails in an encounter per colony per day. Maximum ants lost per encounter is the maximum number of ants per foraging trail times the probability of worker loss per encounter. The number of foragers per trail is based on the maximum numbers of foragers per unit time passing a point on a foraging trail in colonies of known age (Gordon 1988, 1991, 1992*a*). We estimated how many ants it would take, moving at a speed of 2.5 m/min (typical of peak foraging temperatures), to fill the maximum length of foraging trails measured in colonies of that age (Gordon 1992*a,* 1995). The probability of worker loss per encounter is the probability a forager will engage in a fight times 0.21, the probability of death or injury in a fight. To calculate the probability a forager will engage in a fight we used data from a previous study (Gordon 1991), in which seed was placed between each of seven neighboring pairs of colonies aged 3 yr and older. Over 9 d, in 40 encounters with fighting, the numbers of ants per colony seen fighting in one trail's encounter at one time ranged from 1 to 16; the average was 4.1. To find a maximum probability a forager will fight we assumed an average of 10 fighters and an intermediate value of 800 foragers per trail (Table 5). The probability a forager will fight is estimated to be 10/800, or 0.0125. The probability of worker loss per encounter is thus (0.0125)(0.21) = 0.002625.

It appears that average yearly losses due to fighting range from 151 ants in a 1-yr-old colony to 990 in a colony 5 yr or older (Table 5). When a large colony is excavated in midsummer, there are usually ≈2000 brood present (larvae and pupae) (MacKay 1981 for *P. rugosus,* with colonies of similar size; Gordon 1992*a* for *P. barbatus*); thus the amount of brood present in midsummer could easily replace the year's loss of ants to fighting. By contrast, Munger (1984) found that ≈200 ants are taken in each bout of predation by horned lizards on *P. desertorum,* and *P. barbatus* probably loses more ants to predation than *P. desertorum.* Thus for a large *P. barbatus* colony, five predation episodes would probably be more costly than all its yearly losses due to fighting with conspecific neighbors.

The cost of conflict between neighboring colonies calculated here is much lower than that postulated in previous studies of a variety of ant species (Holldobler 1976, De Vita 1979, Holldobler and Lumsden 1980, Adams 1990). Most theoretical models of territorial behavior also postulate greater losses than those indicated by this study (e.g., Schoener 1983; reviewed in Marden and Rollins 1994).

It is possible that frequent interaction diminishes the survivorship of founding colonies. First, though the costs of interaction as measured here are small, these costs might still decrease a colony's chance of survival. Second, there may be other costs of interaction that this study has overlooked.

An alternative explanation is that exploitative competition, more than interference competition, influences the spatial distributions of nests. Colonies meet when they forage in the same place at the same time. But the two colonies may also forage in the same place at different times. Colonies use several foraging directions each day from a set of habitual trails (Gordon 1991); on the time scale of weeks, a colony may use the same foraging directions many times (though directions are often not preserved from year to year [Gordon 1995]). The probability that two colonies will meet thus reflects the probability that they will exploit the same foraging area, even if not on the same day. Renewal rates are low: *P. barbatus* collects seeds distributed by wind and flooding, often produced many months previously (Gordon 1993). More frequent interaction between two colonies implies more overlap in foraging area over the course of a season.

Interaction itself is related to the probability of further overlap in use of foraging area. Once a colony meets a neighbor, the two colonies are likely to meet and search the same foraging area again the next day. Since older, larger colonies are more likely to meet their neighbors than younger ones, repetition of encounters tends to reinforce the competitive pressure of older, larger colonies on younger, smaller ones.

Competition for space may be linked to colony life history. Once a colony has reached 2 yr of age, it is likely to live another 15 or so years. It has a cohort of neighbors with whom it will have to partition foraging space for the next 15 yr. A 3–4-yr-old colony is generally at the steepest point in its growth curve, when food intake must be high to maintain a large larva/worker ratio; this may explain its persistence in conflict with neighbors. Once the colony reaches ≈5 yr old, it has reached the size it will maintain for the rest of its life, and it begins to reproduce (Gordon 1995). Nest excavations suggest that seed stores in large colonies can be substantial (D. M. Gordon, *personal observation*). Food supply may determine colony growth and the number of sexuals produced (Topoff and Mirenda 1980, MacKay 1985, Elmes 1987, Munger 1992, Tschinkel 1993). Older, larger colonies may eventually obtain the seed stores necessary to sustain production of sexual forms without having to engage in frequent conflict with neighbors.

However, in very crowded regions, such as the area between ≈0–100 m east, 75–125 m north of the study site (Fig. 1), conflict may well be detrimental to older colonies. Many colonies were successfully founded in this area in 1988, 1989, and 1990 (Fig. 1). In 1993 and 1994, few of the older colonies in this area were seen to produce sexual forms, and all appear to be unusually small for their age. Intense competition, due to crowding, might have prevented the growth necessary to reach the reproductive stage of the life cycle. Work is currently underway to measure reproductive success in *P. barbatus* colonies and to formulate a spatially-explicit evolutionary model of life history changes in colony–colony interactions.

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