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The effect of neighbours on the mortality of harvester ant colonies

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Summary

1. This study investigates how the density and size of conspecific neighbours affected the mortality of established colonies. Data were from a population of 250–300 colonies of the red harvester ant [*Pogonomyrmex barbatus* (F. Smith)], on a 10-ha site, from 1988 to 1995.
2. Colonies are more likely to die as they grow older.
3. Small neighbours tend to lower the probability of dying.
4. The probability of dying varied significantly from year to year.
5. There was little effect of crowding on mortality.
6. There appeared to be no spatial effects, on the scale of 25 m, on the probability of dying.
7. Previous work shows effects of density on the founding of new colonies and on the reproductive output of established ones. The results presented here indicate that competition with neighbours rarely causes the death of established colonies.

Key-words: colony size, density dependence, mortality, seed-eating ants.

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Introduction

When a population uses a limiting resource, recruitment, fecundity or mortality may be density dependent. The age structure of a population can influence the outcome of resource competition (Tschumy 1982; Caswell 1989; Siegismund, Loeschke & Jacobs 1990). An individual's size and age determines its use of resources (Werner & Gilliam 1984). Individuals may be especially vulnerable to competition at particular stages of the life cycle. Density-dependent mortality because of resource competition is well known in many animals (Owen-Smith 1990; Clutton-Brock *et al.* 1991; Bohlin *et al.* 1994), but there are few empirical studies of age-specific density dependence in animal populations (Desharnais & Liu 1987; McDonald, Fitzpatrick & Woofenden 1996). In plants and sessile animals, competition has a spatial component (Pacala & Silander 1985; Roughgarden, Iwasa & Baxter 1985), and the effects of age structure result from the way each individual's age-specific resource use interacts with that of its neighbours. Here we ask how mortality is related to density and age in a population competing intraspecifically for space.

Given the ubiquity and abundance of ants, there have been surprisingly few studies of their population dynamics (Pontin 1969; Elmes 1987; Tschinkel 1993). Little is known of the effects of age structure on the dynamics of ant populations, because long-term data are needed to determine the ages of individual colonies. However, even in the absence of data on colony age, it is often possible to distinguish newly founded colonies from older ones. Several studies have shown that the survival of new, small colonies is threatened by proximity to conspecific neighbours (Ryti & Case 1988; Adams & Tschinkel 1995; Wiernasz & Cole 1995; Gordon & Kulig 1996). Thus in a few genera of ants, at least, it is clear that competition influences the recruitment of new colonies. Much less is known about the demography of established colonies, and how interactions among established colonies affect population dynamics.

This study draws on data on a population of about 250 colonies of the red harvester ant (*Pogonomyrmex barbatus*) censused each year since 1985. Colonies live for 15–20 years (Gordon 1991). New colonies are founded by queens that disperse after mating at an annual mating aggregation. Since in this species new colonies do not form by budding, and it appears that newly mated queens disperse at random from the site of the mating aggregation, there is no evidence that neighbouring colonies are closely related. A colony is founded by a single queen, grows to a size of about 10 000 ants and begins to reproduce when it is about

5 years old (Gordon 1992a, 1995), and remains at this size for the next 10–15 years. When the queen dies and the remaining workers, who live about a year (Gordon & Holldobler 1988), have died, the colony is dead. Newly mated queens are not adopted by existing colonies.

Neighbourhood density and the size of neighbouring colonies affect the recruitment of new colonies and the fecundity of mature ones. Mortality of newly mated queens and newly founded colonies is extremely high, apparently more than 90% (Gordon & Kulig 1996). The probability that a founding colony will become established at a given site (surviving to be 1 year old) depends on the density of other colonies at the site (Gordon & Kulig 1996; Wiernasz & Cole 1995 for another harvester ant species). Survival of new colonies further depends on the sizes of neighbouring colonies (Gordon & Kulig 1996): a founding colony is most likely to survive to 1 year at a site crowded with small, young colonies. Neighbourhood density affects the reproductive output of mature colonies; more crowded colonies produce fewer reproductives (Gordon & Wagner 1997). The effects of neighbours on recruitment and fecundity both appear to be due to competition for foraging area (Gordon 1991, 1992b).

Neighbours may influence a colony's survival even after its first year, and the size of neighbours may be important. Overlap of foraging area is most frequent with neighbouring colonies that are old and large (Gordon & Kulig 1996), and colonies of intermediate, prereproductive age are the most persistent in their use of contested foraging areas (Gordon 1992a; Gordon & Kulig 1996). The present study examined how density and neighbour age/size affect age-specific colony mortality.

Methods

A population of colonies in a 10-ha plot was mapped and censused each summer from 1985 to 1995. Details of censusing methods are given in (Gordon 1987, 1991, 1992b, 1995). Colony age is known or estimated using this census. In 1985, some colonies were estimated to be 5 years or older by comparison with the nest size of other colonies of known age. For most new colonies established on the site since 1985, the age is known.

Colonies are considered to be 1 year old, founded in the previous summer's mating flight, the year they are first included in the census. Data for newly founded colonies that appeared the summer they were founded but were gone the next year, when they would have been 1 year old, are not included in this study.

About 10% of nests move each year (Gordon 1992b). The ages of colonies that moved onto the study site from outside the mapped area were estimated on the basis of colony size; the numbers of such colonies are shown elsewhere (Gordon & Kulig 1996; Table 1). Nest relocation usually occurs after the summer rains, during the time when one of us (DMG) has been present at the study site each year since 1985. Nest relocation is a lengthy and dramatic process (described in detail in Gordon 1992b), and most moves have been observed. However, some colonies apparently moved at a time when the authors were not present at the site, mostly after unusually heavy spring rains. In these cases we found an unoccupied nest mound that was active the year before, and near to it a large colony that was not there the year before, obviously older than 1 year and apparently of the same age as the colony that was in the unoccupied mound. This study used data from 1777 colony-years, of which 60 colony-years (3%) were from 21 colonies of questionable age because of presumed nest relocation. Of these 60 colony-years, there were 25 from 11 colonies in which the original colony could be identified with high probability. For the remaining 10 colonies and 35 colony-years, we guessed the identity and thus the age of the relocated colony. Two kinds of evidence contributed to these guesses: (i) the same colonies tend to move year after year (Gordon 1992b);

Table 1. Number of colonies by age and year. Numbers of colonies that died are shown in parentheses

Colony age	1988	1989	1990	1991	1992	1993	1994	Total
1	25	42	19	30 (1)	17	37 (6)	7	177 (7)
2	8	28	49 (1)	38	35 (3)	21 (2)	36 (1)	215 (7)
3	30	11	33 (2)	54 (1)	35	38 (1)	20 (1)	221 (5)
4	20	30	12 (1)	32 (3)	49 (3)	33 (2)	35 (2)	211 (11)
5	22	27 (1)	30 (1)	13	32	43 (6)	30 (3)	197 (11)
6	16 (1)	22	25 (2)	28 (2)	12	31 (1)	40 (3)	174 (9)
7	8	15 (1)	19 (4)	25	26 (2)	11 (1)	29 (1)	133 (9)
8	16	8	11 (3)	18 (1)	24 (1)	24 (2)	11	112 (7)
9	0	16	8	9 (2)	18	21 (3)	24 (1)	96 (6)
10	0	0	12 (4)	8	9	16 (2)	21	66 (6)
11	0	0	0	11 (1)	7 (1)	9 (1)	15 (1)	42 (4)
12	0	0	0	0	9 (1)	5 (2)	9	24 (3)
13	0	0	0	0	0	10 (1)	5	14 (1)
14	0	0	0	0	0	0	9	9 (0)
Total	145 (1)	199 (2)	218 (18)	266 (11)	274 (11)	298 (30)	291(13)	

and (ii) colonies move along foraging trails, and sometimes we had maps of these for the previous year (Gordon 1995).

A colony persists and continues to forage after the queen has died, until all of the workers have died. The queen of a colony found to be dead in a particular summer could have died anytime in the preceding year. Here a colony is considered to be dead when the nest entrance is closed, the mound is overgrown, there is no response to scratching with a twig inside the nest entrance (which often brings out the ants from a live but inactive colony), and no ants are seen to emerge from the nest in checks made on at least five different days. There is considerable day-to-day variation in foraging activity; colonies tend to be active on the same days (Gordon 1987, 1991). The checks of colonies that might be dead were made each year on days when foraging activity was high and colonies were most likely to be active, usually days following rain. About half the colonies that appear inactive, and possibly dead, in the first observations of the season, prove to be alive in the course of subsequent checks.

This study uses data on colony mortality for 7 years from 1988 to 1994 (Table 1). In the data analysis, the year of death is considered to be the year before the one in which the colony is found dead. Thus, for example, a colony assumed to be 1 year old when it died was found dead the summer it would have been 2 years old.

To reduce spatial edge effects, the survival rates for colonies within borders chosen to exclude colonies lying at the edges of the study site were modelled (shown in Gordon & Kulig 1996, Figure 1). Colonies outside the arbitrarily chosen borders were used only to calculate neighbour information for colonies within the borders.

Logistic regression was used to model the effect of neighbours on the probability that a colony dies within a given year. Explanatory variables tested were: year; distance from the colony to its fifth nearest conspecific neighbour; the number of conspecific neighbours within 20 m of the colony; age of the colony; and the number of the five nearest neighbours that were aged 1 year, the number that were aged 2 years, and so on for ages 3, 4, 5 and 6 years or older. To measure the effect of location, the colony's east and north coordinates, each of these squared, and their product, were included as explanatory variables.

Distance to the fifth nearest neighbour was chosen as a measure of density because studies of foraging behaviour indicate this measure probably reflects the extent of competition for foraging area more accurately than the number of colonies per unit area. Neighbouring colonies meet when the foragers of both search the same area for food (Gordon 1991, 1992a). In a previous study, 34 colonies were observed for 17 days (Gordon & Kulig 1996). In about half of these 34 colonies, foragers encountered the foragers of the fifth nearest neighbour, and 75% of all encounters with foragers of another colony were with one of the five nearest neighbours. When neighbouring colonies search the same area, a trail of one colony does not cross that of a neighbour and continue on the other side. Thus a colony's foraging area is bounded by the trails of those neighbours it is likely to meet, usually its five nearest neighbours. A measure of density that included neighbours beyond this range would tend to include colonies that have no effect on resource use. The present study tested a second measure of crowding, the number of colonies located within 20 m, because colonies rarely meet others more distant than 20 m (Gordon & Kulig 1996).

Year was included as an unordered factor, because both year and year^2 as ordered variables were not significant in a preliminary analysis; there was no monotonic temporal trend in the data. To identify the intercept term in the regression, we defined the coefficient for 1988 to be 0.

Age of the colony was included as a linearly ordered factor with levels of 0, 1 and 2 representing ages 1–3 years, 4–9 years and 10 years or older (Fig. 1). Colonies were grouped into age classes because, for colonies first mapped in 1985, estimated to be at least 5 years old in 1985, the ages are not known with certainty. The grouping was chosen by inspecting the mortality by age results shown in Fig. 1. Linear ordering of the age factor was based on an initial regression of the probability of dying on age with the three levels listed above, which yielded estimated coefficients of 0, –0·6, and –1·07 that, when plotted, form a nearly straight line. The ratio of colonies of a given age that died to colonies that did not die was 0·03 for colonies 1–3 years old, 0·05 for colonies 4–9 years old and 0·08 for colonies 10 years or older.

Logistic regression models the log of the odds ratio 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 dying by a factor of exp (β), the odds ratio. If β_i is positive, the odds ratio will be greater than 1, and increasing the variable X_i increases the probability of dying. If β_i is negative, the odds ratio will be less than 1, and increasing X_i decreases the probability of dying.

The logistic regression used maximum likelihood estimation of parameters. The set of explanatory variables included in the final model was chosen using a (forward and backward) stepwise selection process based on the approximate χ-squared distribution of the reduction in deviance achieved by adding variables (McCullagh & Nelder 1989). Only terms and interaction terms considered biologically relevant were tested for statistical significance. All analyses were performed with the statistical computer language S.

An assumption of logistic regression is that observations are independent. The probability that a colony survives in a particular year is clearly dependent on whether that colony survived up to the beginning of

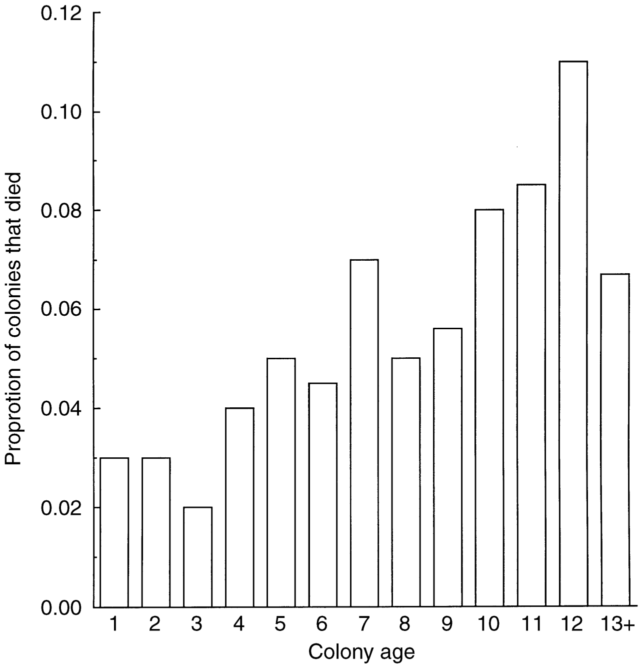

Fig. 1. Proportion of colonies that died. *n* for each bar is the total number of colonies, alive and dead, for each age.

that year. The present study modelled the conditional probability that a colony dies in a particular year, given that it is alive at the beginning of the year. Maximum likelihood estimates of regression parameters and their associated standard errors produced via logistic regression are valid using this conditional probability (Efron 1988). We assume that the probability that a colony dies in a given year is independent of the probability that any other colony dies the same year; while some external factor might cause many colonies to die in a given year, we assume it is not the case that the death of one colony causes the death of the others. The same reasoning applies to external factors that might promote the survival of many colonies in a given year.

To assess the goodness-of-fit of the final model, we calculated a summary test statistic C, which has approximately a χ-squared distribution; a high P-value indicates the model fits the data (Hosmer & Lemeshow 1989).

Three further checks were performed to examine whether the logistic regression gave the same results in subsets of the data. First, the data were divided spatially into two equally sized subsets by a vertical (north–south) line at east coordinate 135 m. The analysis on the western half was repeated with the data from years 1990–94 only (no colonies died on this side in 1988–89). Second, two subsets of the data were analysed separately: for years 1988–91, and for years 1992–94. Third, the results suggested that, in some years, mortality was reduced for colonies with small, 2-year-old neighbours. To test whether this result was unduly influenced by the data for 1988 and 1989, during which the three colonies that died had no 2-year-old neighbours, the analysis was repeated, omitting the data for these 2 years.

To test the adequacy of the final model of the logistic regression, we performed a parametric bootstrap test (Efron & Tibshirani 1993): data were generated from the estimated model and then used to re-estimate model parameters. By repeating this process many times, the distribution of the deviance of the bootstrapped data from the re-estimated model can be approximated, and then compared to the original deviance for the fitted model to test the null hypothesis that the estimated model is correct. An estimated P-value then is the percentage of bootstrapped deviances that are larger than the deviance for the fitted value; a P-value $> 0{\cdot}05$ indicates the null hypothesis cannot be rejected.

The logistic regression tested whether the risk of mortality changes along an eastward or northward directional gradient. To check whether the risk of mortality is higher in particular locations or patches of the study site, deviance residuals after fitting the model were plotted in space (Fig. 2). Before plotting, the deviance residuals were first smoothed using a Gaussian kernel smoother with a window width of 25 m (Silverman 1986). We used deviance residuals because they were also used in choosing the final model. Spatial dependence in the data not captured by the model will appear as hills or valleys on the plot. Trends consistent from one year to the next should appear in the same place on successive plots.

Results

The overall probability that a colony dies in a given year is the ratio of colonies that died to colony-years, or $0{\cdot}048$ ($= 86/1777$). This is also the average of all of the probabilities of dying, estimated separately for each explanatory variable by the logistic regression.

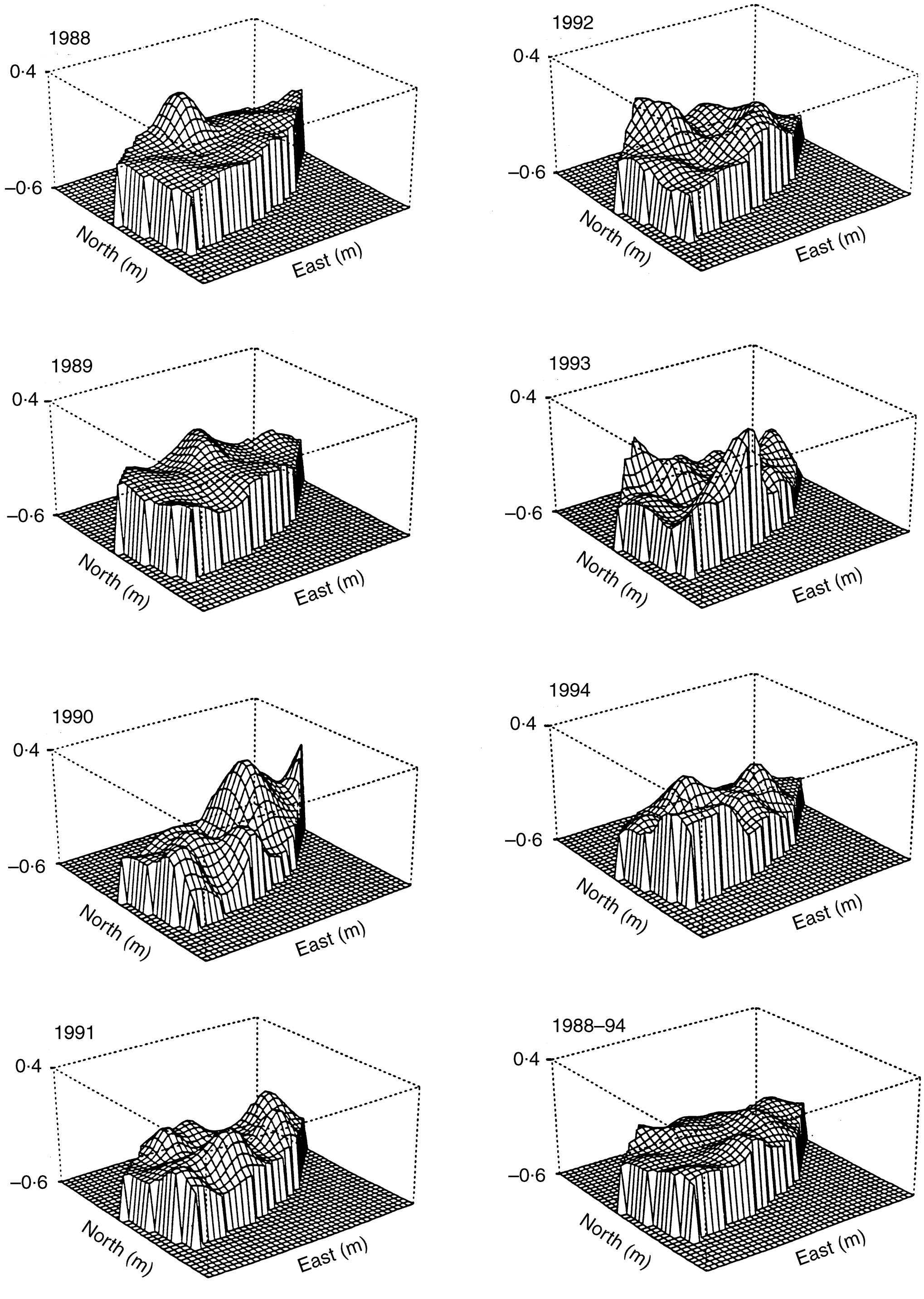

Fig. 2. Spatial distribution of the probability of dying each year. The raised area, representing the study site, measures ≈ 400 × 240 m. The vertical axis shows the smoothed deviance residuals obtained after fitting the final model of the logistic regression. Residuals are positive where more colonies died in the surrounding location than predicted by the logistic regression, and negative where fewer colonies died than predicted. Residuals were smoothed using a window width of 25 m.

The probability that a colony will die in a given year depends on its age; colonies are more likely to die as they grow older (Fig. 1). The odds ratio for dying as a colony moves from one age class to the next (1–3 to 4–9, or from 4–9 to 10 or older), was 1·594 (= exp(0·461)) (Table 2). The study did not examine statistically the variation in mortality within the years of a given age class. There was no interaction of colony age class and the age/size of its neighbours, indicating that, as the colony ages, there is no change in its vulnerability to competition with neighbours.

Small neighbours tend to lower the probability of dying. The effect on mortality of the number out of the five nearest neighbours that were 2 years old, varies from year to year (2-year-old neighbours × year interaction, Table 2). The estimated odds ratio associated

Table 2. Results of logistic regression

Explanatory variable	Coefficient	d.f.	P
Final model			
Intercept	–4·968	1	–
Year:		6	< 0·001
1988	0·000		
1989	0·756		
1990	2·549		
1991	1·631		
1992	1·985		
1993	1·999		
1994	1·600		
Age	0·461	1	0·007
Number of 2-year-old neighbours	–5·177	1	0·031
Year × Number of 2-year-old neighbours:		6	0·035
1988	0·000		
1989	–0·006		
1990	4·624		
1991	4·898		
1992	3·849		
1993	5·781		
1994	4·723		

with an increase of one in the number of 2-year-old neighbours among the nearest five cannot be meaningfully estimated for 1988 and 1989, since the colonies that died in these years had no 2-year-old neighbours within the nearest five. For each year from 1990 to 1994, the odds ratios associated with an increase of one in the number of 2-year-old neighbours were 0·575, 0·757, 0·265, 1·828 and 0·635. (The odds ratio for a given year is $\exp(-5{\cdot}177 + a)$, where –5·177 is the estimated coefficient for the overall effect of number of 2-year-old neighbours, and a is the coefficient for the interaction of year × number of 2-year-old neighbours for that year; for example, the odds ratio for 1990 is $\exp(-5{\cdot}177 + 4{\cdot}624) = 0{\cdot}575$ (Table 2)). Thus for 4 of the 5 years, with 1993 the exception, the odds ratios are less than one, indicating that small neighbours decreased the probability of dying.

The probability of dying varied significantly from one year to the next (Table 2). Taking other explanatory variables into account, 1988 had the lowest estimated overall probability of dying and 1990 had the highest; their estimated coefficients, 0 and 2·549, are the lowest and highest of the estimated coefficients for the year effect (Table 2). To illustrate how much years can differ in the probability of dying, the estimated odds ratio for the probability of dying between years 1988 and 1990 was 12·795 ($= \exp(2{\cdot}549 - 0)$). Because of the interaction of year and the number of 2-year-old neighbours, this odds ratio is for colonies with no 2-year-old neighbours.

There was no effect of crowding on mortality, when crowding was measured either in distance to the fifth nearest neighbour or number of neighbours within 20 m. There was no effect of neighbour age for ages other than 2 years. There was no apparent directional gradient within the study site in the probability of dying, because there was no effect of the values of the E coordinate, N coordinate, their values squared or their product.

The test statistic C ($C = 4{\cdot}086$, d.f. = 8, $P = 0{\cdot}85$) indicates a good fit for the regression model.

The results for the logistic regression were not strongly affected by the paucity of colonies that died in the first 2 years. When the first 2 years of data were excluded, the effects of year and colony age were still significant, and the number of 2-year-old neighbours was nearly significant at $P < 0{\cdot}054$. All variables had estimated coefficients nearly equal to the estimated coefficients using the full dataset.

Factors affecting mortality differed in 1988–91 and 1992–94, and in the two halves of the study site. Mortality depended on colony age in the earlier years of the study, and on the western half of the study site. The effect of colony age was highly significant for 1988–91 ($P < 0{\cdot}001$), with an estimated coefficient (1·004) about twice as large as that for all 8 years (0·461, Table 2); by contrast, there was no significant effect of colony age in 1992–94 (coefficient 0·15, $P = 0{\cdot}5$). In the western half of the study site, there was a significant effect of age (coefficient 0·567, $P < 0{\cdot}01$); in the eastern half, the effect of age was not significant (coefficient 0·357, $P = 0{\cdot}13$).

The number of 2-year-old neighbours within the nearest five had a significant effect on mortality in 1988–91 (coefficient –0·485, $P < 0{\cdot}05$), but not in 1992–94 (coefficient –0·137, $P = 0{\cdot}5$). The number of 2-year-old neighbours was not significant when either the eastern or western half of the study site was considered separately (coefficient –0·382, $P = 0{\cdot}09$ for the eastern half; coefficient –0·319, $P = 0{\cdot}12$ for the western half), although the coefficients for each half were both negative, as was the coefficient for the whole site combined.

The effect of year was significant in 1988–91, 1992–94, and in the eastern half of the study site, but was not significant in the western half.

The number of colonies within 20 m had a significant effect on mortality in the eastern half of the site (coefficient 0·158, $P < 0{\cdot}05$), although it had no significant effect for any of the other subsets of the data or for the full dataset.

The parametric bootstrap test of the adequacy of the model resulted in 398 out of 1000 bootstrapped deviances greater than the deviance of the final model, for a P-value of 0·39; the deviance from the final model was consistent with the distribution of bootstrap deviances. This P-value > 0·05 indicates that we cannot reject the null hypothesis that the model is correct.

Plots of the smoothed deviance residuals for each year indicate that there are no patches on the study site, on a scale of 25 m, where the probability of dying is consistently high or low, year after year (Fig. 2).

Discussion

Harvester ant colonies appear to have little effect on the mortality of their large, established neighbours. Few older, established colonies actually die as a result of competition for food with their neighbours. Previous work shows that the more crowded a colony's neighbourhood, the more likely its foraging range will overlap with those of its neighbours (Gordon & Kulig 1996). More crowded colonies also produce fewer alate sexuals (Gordon & Wagner 1997). Both these results suggest that crowding is inversely related to food intake. Crowded colonies appear not to grow in size as quickly as less crowded colonies of the same age (DMG, personal observation); perhaps a reduced food supply limits a colony's production of workers as well as alates. Even with intense competition for food, most colonies may find enough food to continue feeding the queen and produce some workers, so that the colony does not die. These results are consistent with those of Wiernasz & Cole (1995) for a related species, *P. occidentalis*. Using 1 year's data in a large population in which colony age was not known, they found no relation between density and mortality.

In some years, it may be more difficult than in others for colonies to find enough food to survive. There was a significant effect of year on mortality in all the analyses performed here, on the entire data set and on most subsets of the data. Most seeds collected by ants at this site are distributed by wind and flooding (Gordon 1993), and seed abundance varies strongly from year to year (Kemp 1989). Yearly variation in mortality may be related to yearly variation in food supply.

In some years, colony survival may be tenuous enough to be threatened by competition from neighbours. The interaction of year and number of 2-year-old neighbours suggests that, in some years, a colony's chances of surviving are enhanced if it has young, small neighbours. These small colonies are less likely than larger ones to overlap with neighbours in foraging range (Gordon & Kulig 1996) and more likely to retreat from encounters between colonies (Gordon 1992a). Several results show that the positive effect on survival of 2-year-old neighbours is a weak one; the effect was reversed for 1993, it was not significant in the last 3 years of the study (1992–94), and it was not significant for either half of the study site considered separately.

It appears that the effect of density is stronger when colonies are less crowded. When subsets of the data were analysed, effects of crowding were more important in the less crowded half of the study site (the eastern half) and during the less crowded years (1988–91) The average number of colonies within 20 m was 4·3 for the eastern half and 6·2 for the western half of the site. In the eastern but not western half of the site, mortality increased significantly with number of neighbours within 20 m. Similarly, the effect of number of 2-year-old neighbours was significant in the years 1988–91 when colonies were relatively less crowded, with an average of 4·5 colonies within 20 m, than they were from 1992 to 94, with 5·9 colonies within 20 m.

It is interesting that there was an effect of crowding at lower densities. A speculative explanation is that allocation to worker or reproductive production depends on food availability during some critical period early in the colony's life history. At lower densities, resources may be more abundant, and colonies may choose a more costly life history alternative, such as more worker or reproductive production at an earlier age. Once the colony is committed to this course, however, competition from neighbours may deplete resources sufficiently to starve the colony. In crowded areas, colonies may never have the resources to begin reproduction or large-scale worker production (Gordon & Wagner 1997), and without these costs may be better able to survive despite competition with neighbours; further data are needed to test this. At the 10-ha scale of the study site, however, the overall result, that crowding does not affect mortality, should be considered representative, because this result is derived from the largest available sample.

In general, the older a colony is, the more likely it is to die. The effect of colony age on mortality is, however, rather weak, appearing significant only in a large sample of colonies (1777 colony-years). When subsets of the data were considered, mortality depended significantly on colony age only in half of the region and only in some of the years studied.

There is no evidence that particular locations are associated with especially high or low mortality. There was no gradient across the site for the probability a colony dies in a given year. Yearly spatial plots of deviance residuals (Fig. 2) show no consistent peaks or valleys in the same location year after year. The results of this study provide no evidence that variation at the 25 m scale in abiotic factors affects colony mortality.

Density-dependent mortality in a population of harvester ant colonies is similar to the analogous process in a forest. In some tree species, suppression of new trees appears to be more important than mortality induced by competitive interactions of neighbours (West & Borough 1983). Harvester ants are similar to trees in this way; founding colonies are suppressed by established, older ones (Gordon & Kulig 1996) but once a colony is established, its neighbours have little effect on its survival. If a founding queen digs a nest near small neighbours, she is more likely to succeed in establishing a colony. After that first, crucial year, the colony will probably survive for many years even if the neighbourhood is crowded, but it may never manage to reproduce (Gordon & Wagner 1997). Competition for space has been studied enough in plants to reveal some of the ways that species differ in the processes that contribute to spatial distributions. Further work is needed before it is possible to say whether the age-specific mortality of *P. barbatus* is typical of other ant species that establish large, long-lived colonies in fixed locations.

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