

Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality and overdispersion

DIANE C. WIERNASZ and BLAINE J. COLE

Program in Ecology and Evolutionary Biology, Department of Biology, University of Houston, Houston, Texas 77204–5513, USA

Summary

1. The western harvester ant *Pogonomyrmex occidentalis* is frequently the dominant insect species in the deserts and arid grasslands of western North America.
2. The lek mating system of this species provides an opportunity to relate local reproduction to dispersal. Because reproductives from individual colonies aggregate at a limited number of sites for mating, there is a small number of propagule sources.
3. We studied the spatial distribution of a large population of this species. The population as a whole was highly overdispersed, although the patterns of recruitment were highly clumped and correlated in 2 years.
4. In addition to recruitment limitation, we also found evidence of space limitation in the population. Mortality rates were related to the nearest neighbour distance, even when taking into account the fact that small colonies have higher mortality.
5. The spatial structure of the population developed along with the age structure of the population, and was a complex product of the production of new queens, the availability of recruits and the availability of space.

Key-words: age structure, ants, competition, population dynamics.

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Introduction

The spatial pattern of a population is the outcome of two processes: dispersal and survival (Sale & Douglas 1984; Sousa 1984a; Roughgarden, Iwasa & Baxter 1985; Pacala & Silander 1985; Crawley & May 1987; Schupp 1990; Alvarez-Buylla & Garcia-Barrios 1993). For sessile organisms, such as many marine invertebrates and plants, or territorial animals, which are mobile but show high site fidelity, occupancy of a site influences establishment. Recruitment into a saturated population can occur only when physical disturbance or death creates an opening that is free of competitors (Connell 1961a, 1978; Sousa 1984b; Stoner 1990; Clark 1991). Dispersal into such areas may be over the fairly short scales typical of plants (Harper 1977) or the enormously long scales associated with the planktonic larvae of marine organisms (Roughgarden *et al.* 1985), but the survival of a propagule to reproductive age in a population depends on its colonization of empty space.

Prior to the last decade, recruitment was not considered to be an important limiting factor of the population dynamics of communities. However, the incorporation of explicit spatial dynamics into population ecology has caused ecologists to rethink what

processes are important for community structure (Kareiva 1994). Studies of recruitment in marine communities have suggested that, for some species, the supply of propagules may be limiting (Roughgarden, Gaines & Possingham 1988; Danielson & Stenseth 1992; McGarvey, Serchuk & MacLaren 1993). Habitat selection by juveniles or larvae (Stoner 1990; Hurlbut 1991) or deposit of passive young by currents (Reed, Laur & Ebeling 1988; Raimondi 1990; Gaines & Bertness 1993) may produce settlement rates that vary over time or space. Limited dispersal combined with local variation in reproductive output frequently may limit the number of propagules arriving at a site (Roughgarden *et al.* 1988).

If propagules are limited in abundance or localized in distribution, and competitor-free space is also limited and localized, population recruitment will be extremely variable in space and time. It becomes interesting to ask how the spatial patterns of such populations are generated and whether those patterns are at equilibrium. To what extent is the spatial pattern of a population influenced by the availability of propagules versus the availability of space? How often does establishment of new individuals occur? What factors influence the establishment of new individuals?

Monospecific or near monospecific assemblages are uncommon in nature, but provide a convenient venue for studying the production of spatial pattern. Because they are simpler, the set of processes involved in the production of spatial pattern is not confused with interspecific interactions. Many of these assemblages are composed of long-lived plant species growing in physically stressful environments. These include cold temperate or xeric pine forests (Despain 1983; White 1985; Parker 1986), mangrove forests (Chapman 1976), mora forest (Beard 1946) and creosote bush communities (Munz 1974). Studies of these communities have focused on how the dynamics of recruitment, growth and mortality are mediated by conspecifics, as well as what prevents or limits invasion by heterospecific competitors (MacAuliffe 1988; Platt, Evans & Rathbun 1988). Although an implicit assumption or result of most of these studies is often an equilibrium population, typically demonstrated by a stable age distribution, recent work has suggested that these assemblages may frequently not be at equilibrium (Platt *et al.* 1988). This suggests that the population dynamics of monospecific communities may be driven by periodic disturbance or recruitment rather than by intraspecific competition.

Sessile invertebrates and social insect colonies share many features with woody plants. In all three groups, adults are not mobile and occupy an area of the substrate proportional to their size. Survival and fecundity are usually positively correlated with size over most of an individual's life span (Hughes, Ayre & Connell 1992). Although typically on a smaller spatial scale than monospecific plant assemblages, single species of barnacles (Connell 1961b; Bertness 1989) or mussels (Paine 1974; Paine & Levin 1981) may dominate the rocky intertidal, and some coral reefs are composed of single species (Gladfelter 1982; Hunter 1993). Similarly, the nests of social insects, especially termites or ants, may dominate xeric grasslands in Africa, Australia and parts of North America (Wilson 1971). In many of these communities, intraspecific competition for space is thought to be the major organizing process (Connell 1961b; Paine 1966; Dayton 1971; Ryti & Case 1984, 1988a; Hölldobler & Wilson 1990). The patchwork distribution of ants in canopies of tropical forests is characterized by intense aggressive interactions among species (Room 1971; Majer 1976; Leston 1978; Cole 1983a,b; Jackson 1984). Overdispersion of individuals or nests is usually explained as the outcome of such competition (Levings & Traniello 1981; Ryti & Case 1986, 1988b, 1992).

We will present data on dispersion, recruitment, mortality and size structure in a large population of the western harvester ant *Pogonomyrmex occidentalis* (Cresson), in western Colorado, USA. This ant is the dominant insect species in the low deserts of this region. The lek mating system of this species provides an opportunity to relate local reproduction to disper-

sal. Because reproductives from individual colonies aggregate at a limited number of sites for mating, there is a small number of propagule sources. We show that, while the dispersion of new colonies is significantly aggregated, the dispersion of the entire population is uniform. There is evidence both for recruitment limitation and for space limitation in this species.

THE STUDY ORGANISM

The western harvester ant *Pogonomyrmex occidentalis* is one of the most common granivorous ants. The conical nest mounds of *P. occidentalis* are a conspicuous and characteristic feature of deserts and grasslands in western North America. The potential length of occupancy of the nest site is unknown, but these sites can be occupied for very long periods of time (specific nest sites are visible in aerial photographs for at least decades). Studies on this and closely related species elsewhere have reported that colonies apparently have long life spans (15–30 years, Porter & Jorgenson 1988; 43.5 years, Keeler 1982, 1993). Previous studies of small populations (Porter & Jorgenson 1988) have indicated that the distribution of nests is uniform. Colony sizes have been reported to reach a maximum of about 10 000 workers, with the possibility of producing 1000 reproductives annually (in the closely related *P. owyheeii*; Lavigne 1969).

Typically mating occurs annually on a single day. Reproductives fly after heavy rainfall (>5 mm) in midsummer (early July onwards). Mating swarms (leks) occur at the tops of hills, the number and spacing of leks depending on the topography of the area. If a small amount of rainfall (e.g. 1 mm) occurs after a long period without rain, a partial reproductive flight may be observed, followed by the remainder of winged reproductives (alates) flying with the next rainfall. New colonies are begun only by claustral queens; nest budding is not known to occur in this species.

Materials and methods

This study was performed on Bureau of Land Management land approximately 15 km north-west of Fruita (Mesa Co.), Colorado (39° 16' N, 108° 45' W) at 1470 m elevation. The soil is alkaline clay with seleniferous patches and is dominated by saltbush (primarily *Atriplex corrugata*) and greasewood (*Sarcobatus vermiculatus*), both Chenopodiaceae. The site is topographically complex, consisting of six central sets of adobe hills that run roughly north-south. One deep wash, one broad wash (an old road bed) and several shallow washes dissect the site. The common herbaceous species are *Calachortus nuttalli* (Liliaceae), *Castilleja chromosa* and *Penstemon moffattii* (Schrophulariaceae), *Hymenopappus newberryi* (Asteraceae), *Oenothera caespitosa* (Onagraceae),

Oryzopsis hymenoides (Poaceae), and several species of native and introduced crucifers (Brassicaceae).

Our study population consisted of over 1300 colonies of *P. occidentalis* that had been permanently marked with numbered aluminum tags and mapped. One-thousand colonies were tagged in 1992, with extreme care taken to locate all colonies in the area regardless of size. The area of the plot was approximately 27 ha; its boundaries were defined by a gravel road and topographic features. Marked colonies were censused and mapped in 1993; in addition we searched for, tagged and mapped any new colonies that had been founded in the late summer of the previous year. Colonies were mapped by first determining the straight-line distance and compass bearing between pairs of colonies, and then calculating the x and y coordinates of all mapped colonies.

We calculated the nearest neighbour distance for all colonies. In this paper we report nearest neighbour distances from those colonies that were not on the periphery of the study site. The pattern of dispersion was calculated using the test of Clark & Evans (1954). When the sample size is fairly low, the Clark and Evans test is known to bias estimates towards overdispersion, because individuals on the edge of the plot must have nearest neighbours within the plot; potential neighbours who are nearer are excluded. This yields an underestimate of the observed nearest neighbour distances upon which the test is based. Given the sample sizes in our tests, and the exclusion of individuals from the periphery of the plot, we feel that we minimized this source of bias. The Clark and Evans test on nearest neighbour distances was performed both for the entire plot and for the plot divided into 134 quarter-hectare (50 × 50 m) and 40 1-hectare (100 × 100 m) plots. The actual average nearest neighbour distance was computed for those colonies present within each quarter-hectare plot. The nearest neighbours of these colonies were not restricted to being found within the same quarter-hectare plot. This procedure also ameliorated the edge effect bias in the Clark and Evans test.

In general, we did not know the age of most colonies in our population. The exception was 1-year-old colonies. Colonies in their first year after founding have a distinct morphology: a small (less than 25 cm) basal diameter, and a disc instead of a nest cone (height \leq 2 cm). We shall describe the spatial pattern of recruitment in terms of where 1-year-old colonies appeared in the population. To determine whether recruitment was spatially variable between years, we calculated the correlation between the number of first-year nests in 1992 and 1993 for each quarter-hectare plot in our study area, excluding 11 quadrats that included very small sections of the plot. No recruitment occurred in either year in the excluded plots.

We also noted the position of leks in our study area by searching for male aggregations on the day of and the day following the reproductive flight. To provide

some information on the survival probability of foundress queens, in August 1993 we marked the nest entrances of 188 foundresses with wooden toothpicks, and mapped them with respect to established colonies to facilitate retrieval. These nests were checked in March 1994, a time of year when workers in older nests are active, to determine which foundresses had successfully established colonies.

Mortality was scored only for colonies that were tagged in 1992. Nests that had no signs of worker activity and appeared dead were rechecked on several days to verify mortality. Usually, probing with a piece of wire in the nest entrance or blowing in the nest entrance elicited a response if the nest was occupied. A small number of dead nests was noted in 1992, but they were not tagged.

Nest size was placed into six categories in 1992, to facilitate re-identifying marked nests. Nests were categorized as size class 0.2, less than 25 cm diameter; class 1, 25–38 cm diameter; class 2, 38–50 cm; class 3, 50–76 cm; class 4, 76–89 cm; class 5, greater than 89 cm diameter. The size of the nest cone for all colonies was quantified in 1993 by measuring the basal diameter on the north–south axis, on the east–west axis and the height of the nest cone from its base. The size of the nest cone was calculated as the product of the three measurements, and usually presented as the natural log of the product. We calculated the dispersion of seven size classes of colonies (from $\ln(\text{size}) = 6-7$ to $\ln(\text{size}) = 12-13$) using the Clark & Evans (1954) test.

Because we were studying a long-established population of *P. occidentalis*, it was useful to know the degree to which the size of the nest cone predicted the size of the colony. Using excavations, Lavigne (1969) exhaustively determined colony size in the closely related *P. owhyeei*. Although he claimed that external nest did not indicate colony size, his data show a highly significant relationship (correlation = 0.59, $P < 0.001$). To determine whether nest size indicates colony size, we estimated the size of the forager force. Foragers from 31 colonies were collected, cooled on ice, marked with white spray paint and returned to their nests. A range of 20–128 workers was marked depending on the size of the nests. The following day the fraction of marked returning foragers was determined, and worker population size estimated using a simple Lincoln index (Southwood 1978). Although the Lincoln index has several drawbacks for measuring colony size (Porter & Jorgensen 1981), we limited our claim in three ways. First, because we were careful to mark and remeasure only the foragers in the colony, we reduced confounding differences in caste composition among colonies. Secondly, we performed all colony size estimates in less than 1 week, minimizing phenological differences in colony size and worker behaviour. Thirdly, by estimating colony size once, on the day following marking, we reduced the effects of lost markings and worker mortality.

Results

The size of the nest cone was influenced both by size of the colony and the density of colonies. The size of the nest cone was highly positively correlated ($r = 0.88$, $n = 31$, $P \ll 0.001$) with the estimate of the worker force obtained from mark-recapture (Fig. 1). Throughout the rest of the paper, we shall use the nest dimensions as an indicator of the size of the forager force. The size of the nest cone was also positively correlated with the distance between nearest neighbours ($r = 0.31$, $n = 902$, $P \ll 0.001$). Colonies that were close to their nearest neighbour also tended to have smaller nest cones.

The dispersion of colonies was highly uniform (Fig. 2 shows a map of the colonies). This was true

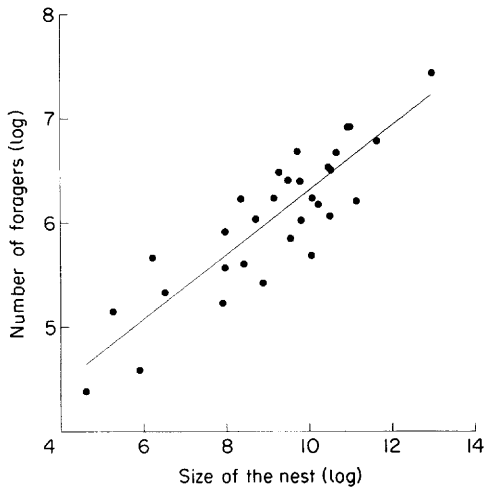


Fig. 1. The relationship between the size of the nest cone (measured as the length \times diameter \times height in cm) and the estimated size of the forager force from mark-recapture. The scale is given in natural log units. The line is the least squares linear regression.

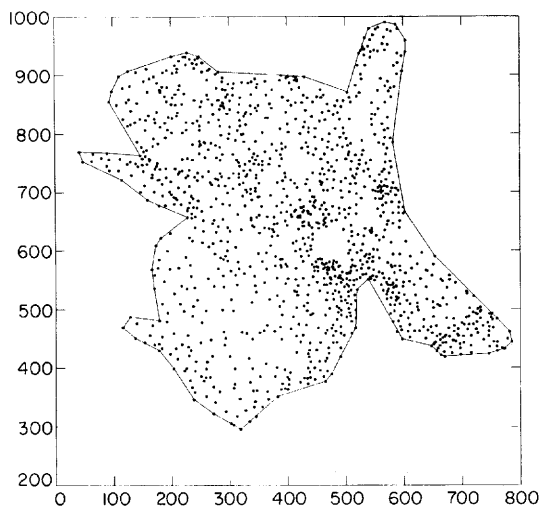


Fig. 2. The map of the study site showing the position of the 1280 nests of *P. occidentalis*. The heavy solid line encloses the area in which the colonies were censused. The interior empty area at coordinates (500, 600) is a region of thick grass that was not censused. North is vertical on the map and the scale on the plot is given in metres.

whether we looked at large or small spatial scales. Over the entire plot, colonies were highly overdispersed ($t = 10.18$, $n = 1029$, $P \ll 0.001$). While the site showed overall uniformity in dispersion, there were patterns that were due both to the size or the age of the colony and which varied across the site. When the study site was broken into 134 quarter-hectare plots (50 m a side) and the spatial distribution of colonies within each plot tested separately, we found that two plots were significantly ($P < 0.05$) clumped and that 24 plots showed significant overdispersion (Fig. 3). We expected that 5% of the tests would be significant by chance alone (expected number = 6.7). The number of plots that were clumped was not significantly different from the number expected by chance ($\chi^2 = 3.47$, $df = 1$, $P > 0.05$); however, the number of plots that were significantly overdispersed was much greater than expected ($\chi^2 = 20.06$, $df = 1$, $P < 0.001$). This test was probably conservative due to the fact that many of the quarter-hectare plots in which colonies were distributed randomly did not have a high enough density of colonies to allow a very powerful test of spatial pattern (number per plot: 9.6 ± 6.4 , mean \pm SD). When we repeated the analysis using 40 1-hectare plots (100 m a side), we obtained similar results: five plots (12.5%) were significantly clumped and 13 (32.5%) were significantly overdispersed. Because the expected number of plots (2.0) at the 5% level of significance was too small to permit a chi-square test, we calculated the 99% confidence intervals for our observed numbers of clumped and overdispersed plots (Snedecor & Cochran 1989). While the observed fraction of plots that was significantly overdispersed was greater than that expected by chance (0.18–0.47), the confidence intervals for the clumped plots included the proportion expected by chance (0.023–0.227).

The probability of successfully initiating a colony

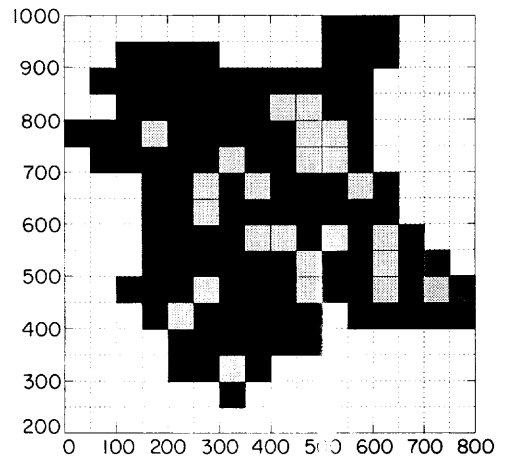


Fig. 3. Quarter-hectare plots coded by whether the colonies were randomly distributed (black), significantly ($P < 0.05$) overdispersed (dark stippling) or significantly clumped in dispersion (light stippling). The scale on this figure are the same as on Fig. 2.

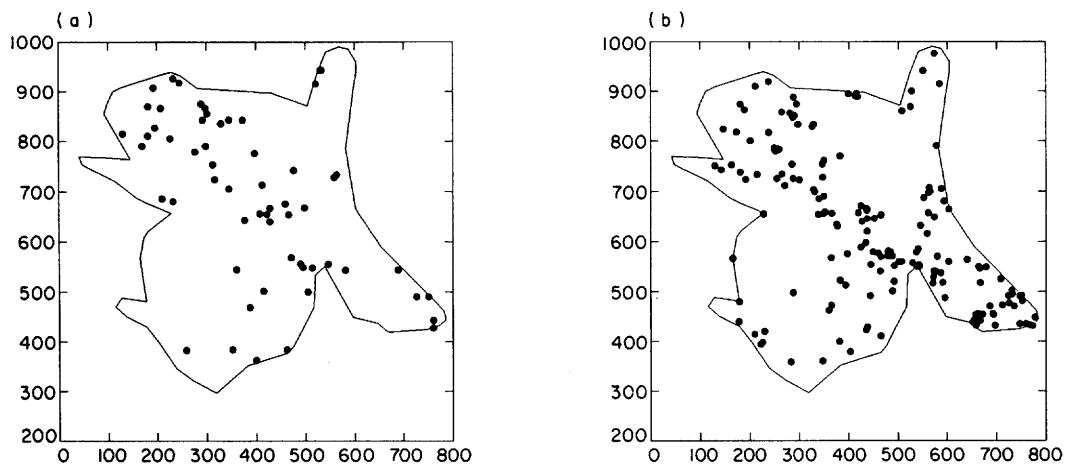


Fig. 4. The pattern of distribution of first-year colonies in 1992 (a) and in 1993 (b). Note the similarity in the pattern of new colonies in the 2 years. The scales of the figure are the same as before. The outline of the plot is given for orientation.

that lives for at least 1 year was low. Of the 188 founding queens marked in July 1993, only two had survived until March 1994. New colonies were not established randomly at our site, instead they were concentrated in particular regions of the plot (Fig. 4). The pattern of distribution of first-year colonies was clumped in both 1992 ($n = 59$ colonies, $t = -2.06$, $P < 0.05$) and, more highly so, in 1993 ($n = 163$ colonies, $t = -5.42$, $P < 0.001$). Initial recruitment was highly spatially correlated across years (Kendall's $\tau = 0.31$, $t = 5.05$, $P < 0.001$, $n = 123$). The clumped pattern of young colony establishment was a function of the foci of recruitment occurring around the lek breeding sites.

Mortality between 1992 and 1993 was not distributed randomly across the site (Fig. 5), but was highly clumped ($n = 86$ colonies, $t = -2.76$, $P < 0.01$). Mortality was associated with two characteristics of colonies. First, the size of the nest was inversely correlated with the probability of death (Fig.

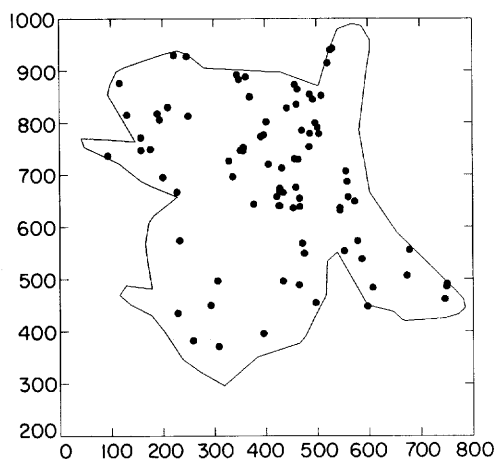


Fig. 5. The pattern of distribution of colonies that died between 1992 and 1993. Note that the distribution of colony mortality differs from the distribution of recruitment. The axes are the same as before.

6a). The probability of dying was highest in first- and second-year colonies (size classes 0 and 1), but declined steeply as a function of colony size. Colonies with a nest diameter of approximately 75 cm (size class >4) had low mortality (2–3% year⁻¹). If a colony achieves this size, it should live at least 30 years. Mortality rate was also a function of the distance to the nearest neighbour (Fig. 6b). Colonies that survived from 1992 to 1993 were, on average, 9.27 m (± 0.16 SE) away from their nearest neighbours. Colonies that died between 1992 and 1993 averaged 7.34 m (± 0.54 SE) from their nearest neighbours. The distance to nearest neighbours was significantly larger among surviving colonies even when the size of the nest cone was taken into account (ANOVA, $F = 13.85$, $df = 1$, 731, $P < 0.001$). This effect was mostly due to survival among new recruits. Mortality in new recruits from 1992 was substantially affected by proximity to neighbours. Surviving recruits were 7.82 (± 0.32) m from their nearest neighbours, colonies that died were 5.93 (± 0.73) m from neighbours ($t = 2.36$, $df = 167$, $P < 0.02$). Surviving larger colonies were on average 9.58 (± 0.18) m from neighbours, while larger colonies that died were 8.42 (± 0.33) m from neighbours ($t = 1.56$, $df = 563$, $P > 0.1$).

Given that recruitment was significantly clumped, and mortality was significantly clumped and associated with both nearness of neighbours and with small colonies, we expected that the pattern of dispersion of colonies would change as a function of the size or age of the colony. Forty-seven of the nests that were 1-year-old in 1992 survived a second year. In 1993 the dispersion pattern of these nests had changed from significantly clumped to random ($t = -1.34$, $P > 0.2$).

The uniform dispersion we observed in this population on both large and small spatial scales did not characterize any particular size category of colony. The Clark and Evans statistic indicated random or clumped dispersion when each size category was tested

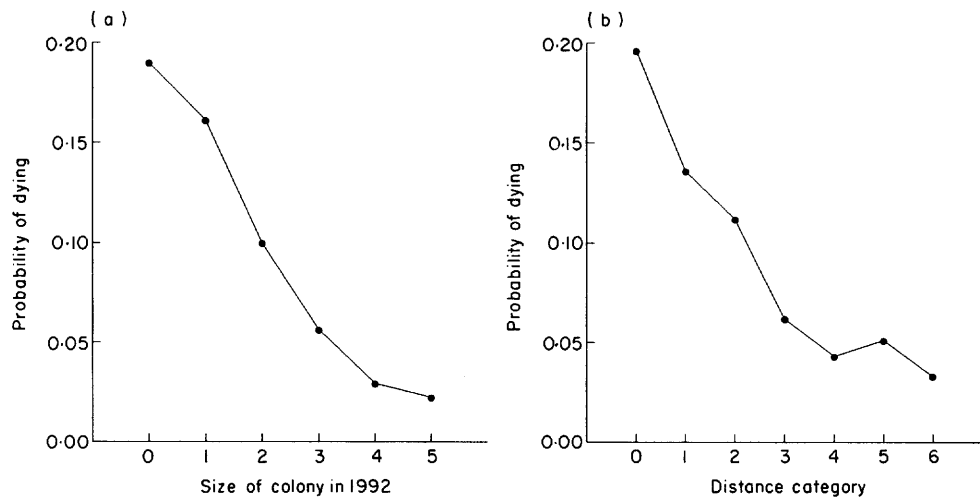


Fig. 6. Mortality between 1992 and 1993 as a function of the size class (see text) of colonies in 1992 (a) and the distance to their nearest neighbour (b). The distance categories are: category 0, less than 2.5 m; category 1, 2.5–5 m; category 2, 5–8 m; category 3, 8–10 m; category 4, 10–14 m; category 5, 14–18 m; category 6, greater than 18 m.

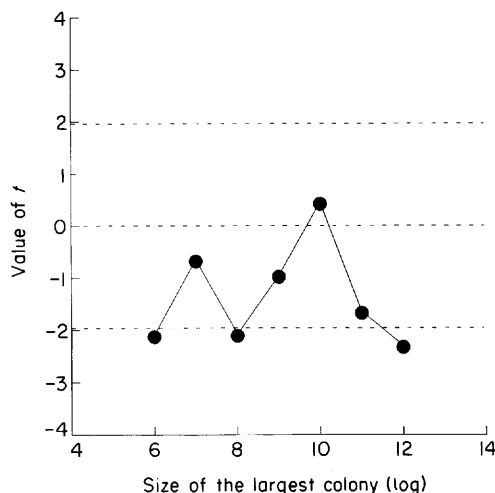


Fig. 7. The t statistic calculated from the Clark and Evans test for spatial distribution for specific size categories of colonies. Values of t above the upper dotted line indicate significantly ($P < 0.05$) overdispersed spatial patterns; values below the bottom dotted line indicate significantly clumped dispersion. The value given represents the dispersion of colonies that are between the given size (see text) and the next smaller size. Although the overall pattern of dispersion is highly overdispersed, each size category is either not different from random dispersion, or significantly clumped.

individually (Fig. 7). Any single size class of the population was not uniform, although the overall pattern was one of extreme overdispersion.

Discussion

In this study, the dispersion of *P. occidentalis* colonies was a function of both spatially heterogeneous recruitment and spatially determined survival. The high spatial concordance of first-year nests between years suggested that the distribution of foundress queens was highly localized in this population. Propagule supply may be limiting for certain regions in the site. The lek

mating system of *P. occidentalis* produces a number of point sources for propagules, the dispersing queens. Lek position is partly a function of topography; we have not observed mating swarms on hills lower than about 7 m. However, the location of leks varies somewhat among years, suggesting that they may be driven by local densities of reproductives. Localized reproduction in marine systems results in similar spatially heterogeneous recruitment (Gaines, Brown & Roughgarden 1985; Reed *et al.* 1988; Raimondi 1990). We expect that the density of foundresses will be a function of the distance from the lek. The clumped distribution of first-year colonies may reflect the original density gradient.

Even though recruitment is highly non-random, intraspecific competition for space erodes the ghost of recruitment past. Initial survival of foundresses may depend on physical aspects of the habitat (e.g. soil hardness, resource availability), proximity of established conspecifics and density of conspecific foundresses. It is possible that the high spatial overlap of first-year colonies in 1992 and 1993 was a consequence of favourable local habitat. Although initial foundress survival must be very low (probably $< 1\%$ of all queens), colonies that survive for at least 1 year are highly aggregated, suggesting that claustral queens do not interfere with each other. Testing these hypotheses will require manipulating the settlement of foundresses (e.g. Ryti & Case 1986). We have, however, shown that long-term survival is mediated by proximity to older colonies; establishment thus depends on the density and spatial array of older conspecifics.

Ants, like many other sessile organisms, are often characterized as being highly space limited (Hölldobler & Wilson 1990). Space limitation (Ryti & Case 1984, 1988a), interspecific territoriality (Hölldobler & Lumsden 1980) and uniform dispersion patterns (Levings & Traniello 1981; Ryti & Case 1986, 1988b, 1992) are often found. We have shown that this pattern of

overdispersion is produced gradually by differential mortality of colonies that are closer to one another. Ryti & Case (1988b) demonstrated a similar changing pattern in the distribution of foundresses in *Messor* and *Myrmecocystus*. This self-thinning process is similar in many regards to that observed in forest systems (Mohler, Marks & Sprugel 1978; Osawa & Allen 1993). We do not know the actual mechanism causing mortality of closely spaced colonies. It could be gradual usurpation of resources by nearby competitors (e.g. Davidson 1985), but this would be unusual for ants (DeVita 1979; Cole 1983a). It is likely to be direct interference competition, resulting in the death of smaller colonies.

Space availability limits establishment in this population in a complicated way. Unlike a forest, when a light gap is opened by the death of a canopy tree, or the intertidal zone, when a beach log kills a patch of barnacles (Dayton 1971), space is never simply occupied or unoccupied. Foragers from surrounding colonies will rapidly fill the gaps created by the death of colonies. Virtually all space in the habitat is filled by foragers from ant colonies (Gordon 1987, 1991). An 'empty' patch produced by the death of a colony is an area where the density of conspecific competitors is lower. Conversely, even in a fully saturated habitat, the density of workers surrounding nests will vary. In low-density areas colonization will have a greater likelihood.

The age structure of the population affects the availability of space and the availability of recruits. Propagules appear in the population in a highly non-random fashion that is a consequence of the limited loci for dispersal. The survival of these new recruits depends strongly on the distance that new queens found colonies from larger, established colonies (Ryti & Case 1988b). The survival of older, larger colonies is not related to the proximity of neighbours. The asymmetry in the effect of nearest neighbour distance on survival results from the extreme differences in the number of workers in established versus newly founding colonies. Recruits to the population are highly influenced by space availability, while older colonies are no longer directly influenced by space. This has the effect of dividing the population into two portions; smaller colonies are competing vigorously for space with each other and with their large neighbours. Larger, older colonies are essentially unaffected by the competition for space that may be occurring among nearby recruits. However, the death of a large colony has a major effect on the creation of space for new recruits. This is similar to canopy trees competing asymmetrically with the seedlings in their understorey (Augsperger 1984). In contrast to forest trees where individuals in the understorey are often the offspring of the overstorey plant, in *P. occidentalis* new colonies are unlikely to be relatives of nearby older colonies.

The spatial pattern of a population is not a property of any age or stage class, but only the overall population.

Dispersion develops with time in an age-structured population. In certain artificial situations, such as experiments, regular spacing may be a feature of the design. By contrast, in natural populations, spacing patterns will develop as a function of recruitment, competition and mortality. If an area of desert is cleared of all *P. occidentalis* and they are allowed to recolonize, recruitment will initially produce a clumped distribution. Non-random mortality, however, will first change this pattern to one that appears random, and eventually to one that is overdispersed. Re-establishment of spatial pattern will depend upon re-establishment of the age structure, and may take at least a century. Although recruitment is clumped due to lek breeding, the site shows little memory of this fact. Reclamation of desert ecosystems may be a lengthy process, not only because the systems are themselves fragile, but because the spatial patterns of animal populations may require long periods of time to develop.

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