

## RECRUITMENT LIMITATION AND POPULATION DENSITY IN THE HARVESTER ANT, *POGONOMYRMEX OCCIDENTALIS*

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**Abstract.** We evaluated the hypothesis that recruitment limitation is important in determining density in harvester ant populations. Combining field observations and experiments, we conclude that the population density of *Pogonomyrmex occidentalis* is largely determined by recruitment limitation, and we demonstrate that variation in population density is a function of the dispersal patterns of foundress queens. The density of established colonies, the number of new colonies, and the number of foundress queens are all highly correlated in this population. The density of foundress queens predicts the density of new colonies in the following year. The density of propagules (foundress queens), new colonies, and established colonies is significantly negatively correlated with the distance from the mating site that is the source of the propagules, and the distance from this source can be used to predict the local density of new and established colonies in this population. Finally, we show that the experimental addition of foundress queens significantly increases the number of new colonies in supplemented vs. control plots. At the landscape level, the population is a mixture of areas with low and high density, with no evidence of overall density dependence. Density dependence is detectable only in local areas that receive sufficient propagules and, thus, depends on the proximity to the source of propagules. Consistent dispersal from a specific geographic site results in variation in population density independent of any variation in habitat quality.

**Key words:** ants; density dependence; density independence; *Pogonomyrmex occidentalis*; population density; recruitment limitation; spatial organization, populations.

### INTRODUCTION

Ecologists have long been interested in how local density is determined in populations (Elton 1927). Density variation can occur as a consequence of local variation in habitat quality. Habitats can vary in quality due to resource differences (e.g., Tilman 1982, Lehman and Tilman 1997), the presence or absence of predators (e.g., Morin 1983, Sousa and Mitchell 1999) or competitors (e.g., Pacala and Silander 1985, 1990, Silander and Pacala 1985, Schmitt and Holbrook 1999), and local variation in the scale and intensity of disturbance (e.g., Denslow 1987, 1995, Coffin et al. 1996, Dalling et al. 1998, Hubbell et al. 1999). Organism survival or habitat selection may result from intrinsic differences in the habitats.

Alternatively, many studies have shown that patterns of immigration or emigration can influence local variation in density (e.g., Hubbell et al. 1999). A number of studies on coral reef fish, marine invertebrates, and trees have suggested that, in some species, the supply of propagules can limit recruitment to the population and thus determine population density (Roughgarden et al. 1985, 1988, Doherty and Fowler 1994, Hurtt and Pacala 1995, Caley et al. 1996, Hubbell et al. 1999). Recruitment in these systems is decoupled from local

processes; new recruits into a population are not found near their source. In several species of barnacles and other marine invertebrates (Gaines et al. 1985, Roughgarden et al. 1988, Possingham and Roughgarden 1990, Stoner 1990, Gaines and Bertness 1992), chronic and consistent limitation of recruitment at specific locations maintains population density below the level that available resources can support.

In mobile organisms, density variation may be a function not only of recruitment, but the degree of habitat selection and the ease with which individuals can move between sites. In organisms with a sessile stage, such as plants, many intertidal marine invertebrates, or ants, dispersal is limited to one stage in the life cycle: pollen or seeds, planktonic larvae, or dispersing queens. In such organisms habitat selection or the movement of dispersing recruits may have long-lasting consequences. Substantial density variation in sessile taxa may be due to intrinsic differences in the local site or to differences in the ability of organisms to reach the site. For example, spatial variation in the availability of resources may either permit higher local density at some sites, or may attract larger numbers of individuals that are capable of choosing among habitats. Even without habitat selection, if propagules are localized, then variation in population density may be due to variation in the numbers of individuals that arrive at a site. In this scenario, variation in local densities arises because some sites simply receive more

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propagules than others. If the propagule supply is low enough it can limit recruitment, and even in long-lived organisms the habitat will not be saturated and density dependence will not be observed.

The circumstance where density dependence may only be apparent at high densities has often been referred to as density vague (Strong 1984, Roughgarden 1997, Turchin 1999). When the density of recruits is so high that it saturates the habitat, further increases in the supply of recruits should not change population density. Below the saturation point, however, a decrease or increase in the density of recruits will produce a corresponding decrease or increase in population density. Above this saturation point, the populations should show evidence of density dependence.

Two alternate explanations, differences in habitat quality or differences in recruitment, can account for variation in the local population density of a sessile organism. This is probably a false dichotomy, and in many systems we expect that both mechanisms operate (Chesson 1998). A more appropriate question is how much of the variation in density is due to variation in recruitment vs. variation in habitat quality. Spatial variation in recruitment will produce several patterns. First, the number of recruits and the number of adults will have a consistent, long-term correlation; areas with high population density will have high numbers of recruits. Because variation in habitat quality can also produce this pattern, a correlation by itself it is not sufficient evidence of recruitment limitation. Second, there will be a geographical feature that promotes or interferes with dispersal, causing consistent variation in the number of propagules arriving at certain locations, ultimately determining density. Third, since resource availability and reproduction play a subsidiary role to dispersal in determining population density, there will only be evidence for local density dependence and spatial variation in the importance of density dependence. Finally, it should be possible to increase population density in some areas by experimentally manipulating the number of propagules at sites that have low density. The last three correlates distinguish recruitment limitation from variation in habitat quality.

Because ants can have high population densities and are territorial and aggressive, they have often been considered a group whose density is limited by space or resources (Hölldobler and Wilson 1990). Ants can affect the local resource base (Davidson et al. 1980, Porter et al. 1988, Porter and Savignano 1990), they interact aggressively both within and between species (Hölldobler 1976a, Cole 1983, Gordon and Kulig 1996), and they are frequently characterized by uniform spatial distributions (Levings and Traniello 1981, Levings and Franks 1982).

Many species of ants, however, have a life cycle that is similar to the open population structure that typifies many marine species. In these ant species, reproduction occurs in large mating swarms that are localized in the

landscape, and queens subsequently disperse from these point sources. The habit of localized mating and dispersal effectively decouples local offspring production (of queens and males) from local propagule acquisition (return of dispersing queens). Because there is a dispersive juvenile stage and a sessile adult stage, there is a possibility that local population density may be affected by the availability of recruits.

We evaluated the importance of variation in recruitment for variation in population density in the harvester ant, *Pogonomyrmex occidentalis*. We compared the density of foundress queens (propagules), 1-yr-old colonies (recruits), and established colonies (>1 yr old) as a function of distance from dispersal sites to determine how propagule supply affects colony density. In low-density areas we supplemented propagules to try to increase recruitment. We used three fitness correlates to look for evidence of density-dependent processes at local scales.

#### MATERIALS AND METHODS

*Pogonomyrmex occidentalis* is a seed-harvesting species that is frequently abundant in the arid lands of western North America. Colonies are uniformly distributed, although there is considerable variation in population density (Wiernasz and Cole 1995). *P. occidentalis* is a swarm-mating species: queens fly to hilltop mating aggregations from their natal colony, and disperse individually after mating, to commence solitary colony founding (Nagel and Rettenmeyer 1973, Hölldobler 1976b, Wiernasz and Cole 1995, Wiernasz et al. 1995). Mating flights are triggered by midsummer rainfall. In western Colorado, where this work was conducted, *P. occidentalis* typically has one or two mating flights, which may occur from late June to early August (Wiernasz et al. 1995, Abell et al. 1999).

The mating system of *P. occidentalis* decouples local reproduction from local recruitment. The two stages of queen dispersal, flight from their natal colony to hilltops and flight from the mating swarm back to the general population, make it highly unlikely that foundresses establish colonies near their natal nest. Colonies are founded by single, multiply-mated queens (Cole and Wiernasz 1999, 2000a). Unlike some ant species (Hölldobler and Wilson 1990), *P. occidentalis* does not reproduce by budding from established colonies, nor are queens accepted back into their natal nest. In an electrophoretic study of a large population of 960 colonies at this site, we found no evidence of population subdivision (Cole and Wiernasz 1997). Thus, recruitment does not occur in the vicinity of the natal site.

This work was conducted near Fruita (Mesa County), Colorado (39°16' N, 108°45' W) in a study site of ~29 ha in which all colonies of *P. occidentalis* are permanently marked and mapped (Wiernasz and Cole 1995). The study area is subdivided into 135 50 × 50 m (0.25-ha) plots. Of the total plots, 92 are entirely contained within the study site, i.e., not located on the edge of the study site. The entire site was initially

censused (1992) for all colonies, and then for new colonies and mortality of established colonies in annual censuses (June–July) during the next 5 yr (1993–1997). A small proportion of colonies (~1%) relocate in any year. These colonies can be easily distinguished from new colony establishment by their larger size and the co-occurrence of colony abandonment and colony appearance. Colonies were measured each year (number of workers) to determine size and growth (Wiernasz and Cole 1995). Colonies, queen burrows, and hilltops are mapped with a Leica TC600 Total Station (Leica, Solms, Germany) to within 0.03 m from permanent benchmarks established on the study plot.

In this study we define the local neighborhood as the collection of individuals that shares the same ecological site characteristics, and that can directly interact with one another. For different organisms, this means different scales of interaction. We have used 0.25-ha plots to subdivide the study site and approximate the local neighborhood. Density is measured as number of colonies per 0.25-ha plot. At our study site, these plots are also fairly homogeneous in vegetation and topography (over the scales on which the ants forage). Nearest neighbor distances between colonies averaged  $9.2 \pm 4.1$  m (mean  $\pm$  1 SD;  $N = 771$  colonies), and the maximal foraging range is ~30 m, so that colonies on this spatial scale are capable of interacting with one another. Plots of this size also have historical precedents in other studies of desert granivores (e.g., Munger and Brown 1980, Brown and Munger 1985, Davidson et al. 1985).

We subdivided the life cycle of *P. occidentalis* into three stages: queens founding nests, new colonies, and established colonies. Foundress queens begin colonies singly by excavating a burrow that is the nascent nest. The number of queen burrows on a plot established the number of propagules arriving locally. New colonies are those that have survived to 1 yr old. We used the number of new colonies in a plot as a measure of recruitment. Established colonies are older than 1 yr and defined the local population density.

#### *Spatial analyses of recruitment limitation*

To determine whether spatial variation in recruitment occurred in our population, we selected 20 plots that spanned the range of local neighborhood densities at our site. Because we wanted to minimize problems that might arise from spatial autocorrelation, we chose plots that were not adjacent. The number of propagules was determined by censusing the queen burrows on each plot after two reproductive flights that occurred on 29 June and 18 July 1996. Queen burrows are distinguished by the characteristic shape of the entrance hole and the excavated soil. Data from the two queen burrow censuses are combined in this study. To ensure that data were independent, we examined the relation between plot density at the start of the study in 1992 (range 5–24 colonies, median = 12 colonies), the total

number of new colonies (total recruitment) that appeared in a plot in 1993–1996 (range of total recruitment 0–16 colonies, median = 8), the number of queen burrows in 1996 (range of propagules 28–276 burrows, median = 89), and the number of new colonies in 1997 (range of recruitment 0–4 new colonies, median = 1).

The density in 1992 is independent of the recruitment of new colonies in the period 1993–1996, which is independent of the number of queens arriving at a site in 1996. In this paper we use density in 1992 as the sole independent measure of density for analyzing fitness correlates. Since we have density measures for each year we could use average density over the study period, or make separate comparisons for each year. In the first case, density is not independent of subsequent recruitment, and in the second case density and therefore the comparisons are not independent among years. Similar consideration of the need for independence of recruitment and queen density led us to restrict the measures of recruitment to 1993–1996.

Because the queens disperse from hilltops we regressed the number of established colonies, the number of new colonies, and the number of queen burrows in each plot on the distance from each plot to the hilltops. We used the seven hills within and surrounding the study site that were the site of mating swarms in at least one previous year of the study. One hill had mating swarms in every year, while others may have had a mating swarm in only one year. We expected that proximity to a hilltop would be associated with increased density of propagules, recruits, or established colonies, and therefore predicted a negative regression of density on distance and used one-tailed tests. To compensate for multiple comparisons, we applied a Bonferroni correction to establish significance levels.

#### *Propagule supplementation experiments*

Beginning in 1997 we introduced queens into plots historically characterized by low recruitment. Queens were collected in copula at a very large mating swarm located 6 km north of the study site, and held individually in vials in coolers until dusk, when they were released into plots. In 1997 we introduced queens individually into 20 cm diameter arenas placed within three plots that historically had low recruitment ( $\leq$  five new colonies in 1993–1996). Queens were allowed to dig within the arena during the evening after their mating flight; the arena was removed after two days. The three supplemented plots, which each received 100 queens, were paired with a nonsupplemented control plot within 100 m that also had a history of low recruitment. In 1998 we placed 200 queens into the central 20  $\times$  20 m of each of eight plots (including the three used in 1997) without using an arena to confine the queen. We found this to be a more satisfactory technique, because it allowed the queens to select their own site for establishing the nest. Queens could move, although observations suggested that they did not fly

and probably did not move enough to leave the plot. After release at dusk, queens usually ran into vegetation or into cracks in the soil. Each supplement plot was paired with a control plot as above. The experiment was repeated on the same eight pairs of plots in 1999, except that in 1999 we only added 100 queens to each experimental plot. The population level of reproduction was dramatically lower in 1999, which reduced the number of queens available for supplementation. To determine whether queen supplements increased the number of queens attempting to start nests on a plot, the number of queen burrows was counted in six pairs of plots in 1998 within 1 wk of queen addition, and was significantly larger in supplemented plots (one-tailed  $t = 3.60$ ,  $df = 5$ ,  $P = 0.008$ ). Rainstorms erased evidence of queen burrows before all eight pairs of plots could be monitored, but on average there were 42 more queen burrows in supplemented plots. Queen burrows were not counted in 1997 or 1999. Control and experimental plots were monitored for new colonies early in the summer of the following year (1998 or 2000); we found 0–3 (median = 0) new colonies. We analyzed the data by computing the mean number of new colonies in each plot and tested the effect of supplements with a one-tailed Wilcoxon matched-pairs rank sum test, because we expected queen addition to increase recruitment.

#### *Analyses for density dependence*

In each of the plots used in the study of spatial variation in recruitment, we quantified three correlates of fitness. Mortality rate was measured as the cumulative probability of colony death over four years of this study. Since the probability of reproduction is a function of colony size (Cole and Wiernasz 2000b) we used both nest size and colony growth as fitness measures. Nest size, an estimate of the number of workers, is the  $\ln$ -transformed product of the length, width, and height of the nest cone (Wiernasz and Cole 1995, Cole and Wiernasz 2000b); growth is the difference in nest cone size in consecutive years. Because colony growth is a function of colony size (Cole and Wiernasz 1999), we first regressed growth on size for colonies from the entire study area ( $N = 965$  colonies), and then used the residuals of this regression as the standardized growth rate for each colony.

In a stable population, one new colony must be established over the average life-span of a colony. If a local neighborhood is saturated, the density is so high that further increases in the supply of propagules cannot change neighborhood density. If local neighborhood density is not saturated, then there is a balance between recruitment and mortality, and the observed density should be predicted by the number of propagules landing in a neighborhood. Increases in the number of propagules should result in increased recruitment and local density. The predicted  $y$  intercept of this regression is zero. The reciprocal of the probability that

a queen establishes a colony ( $p$ ) is the number of queens that must land on a plot to replace a single colony. Dividing this number by the average lifespan ( $L$ ) of a colony yields the number of queens that must land annually to sustain this rate ( $1/Lp$ ). The reciprocal of the number of propagules that must land annually ( $Lp$ ) is the expected slope of the regression of colony density on propagule number when density is not saturated. If local population density is saturated, then differences in the number of propagules will not be related to density. In this case we predict no relation between the observed population density and the density of the propagules. Since the local population density is stable, it is only in saturated plots that we should see evidence for density dependence.

We used the distribution of propagules arriving at a plot to categorize them as unsaturated or saturated. Our simple criterion was that a plot that received fewer than the median number of propagules was more likely to be unsaturated, while a plot that received more than the median number of propagules was more likely to be saturated. The saturated density was defined as the mean density on plots that received more than the median number of propagules. The average life expectancy in this population is known ( $L = 17$  yr =  $1/\text{annual probability of mortality}$  [Wiernasz and Cole 1995]). We determined the probability that a propagule produced a recruit, and calculated the relation between the number of propagules and expected population density. We then repeated our analyses of density dependence using only saturated plots.

#### RESULTS

The primary requirement for demonstrating spatial variation in recruitment limitation is to show that the density of recruits (new colonies) is associated with propagule density (queen burrows). The density of queen burrows should predict the density of new colonies, and if this is a chronic pattern, the density of new colonies should be correlated with the density of established colonies. The number of queen burrows in a plot in 1996 predicted the number of new colonies produced in 1997 (recruits =  $0.14 + 0.013$  queens,  $r^2 = 0.35$ ,  $P = 0.006$ ,  $N = 20$  plots). If this relationship is forced through zero, and the relationship analyzed as a mixture model (Wilkinson 1996:290–291), the relation is essentially unchanged (recruits =  $0.014$  queens,  $r^2 = 0.35$ ,  $P < 0.0001$ ,  $N = 20$  plots). This relationship is consistent: the correlation between the number of propagules (queen burrows) in 1996 and the establishment of new colonies over the prior four-year period 1993–1996 is highly significant ( $r = 0.67$ ,  $P = 0.001$ ,  $N = 20$  plots, Fig. 1a). The correlation between the number of new colonies established in 1993–1996 and established colony density in 1992 is also highly significant ( $r = 0.74$ ,  $P < 0.001$ ,  $N = 20$  plots, Fig. 1b). When we look at the correlation across the entire 29-ha study site, using only intact plots to ameliorate

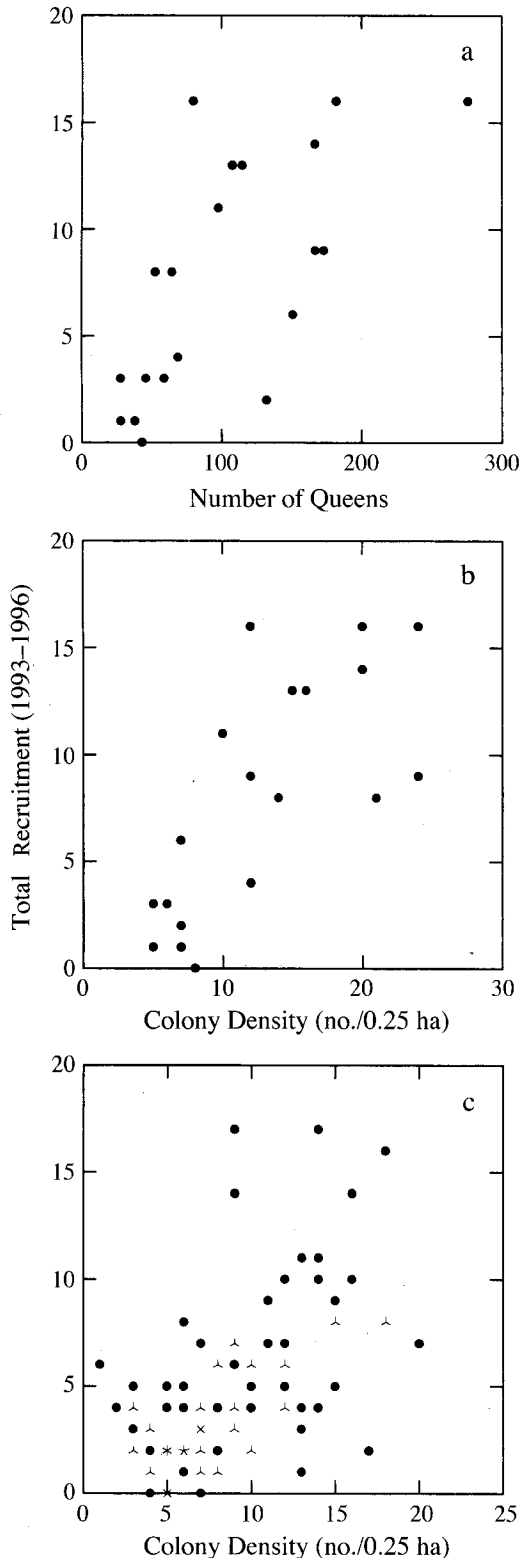


FIG. 1. A study of *Pogonomyrmex occidentalis* demography in western Colorado, showing the number of colonies established on each study plot during 1993–1996: (a) as a function of the number of foundress queens in 1996; (b) for the 20 study plots, as a function of the number of established

edge effects, the relationship between recruitment during 1993–1996 and colony density in 1992 is also very strong ( $r = 0.56$ ,  $P < 0.0001$ ,  $N = 92$  plots, Fig. 1c). These relationships suggest that differences in local population density are associated with long-term differences in the abundance of propagules.

We tested for a relationship between distance to potential mating swarm hills and initial colony density in 1992, recruitment during 1993–1996, and queen burrow density in 1996. We expected that if the distance to the hill was important, there would be a significant negative regression of the density parameter on distance. (As the distance to a hill decreases, the effect of the hill should increase.) The regression of the density parameter on the distance to Hill 7 was significant in all of the following three cases: colony density ( $P = 0.025$ , Fig. 2a; in all cases  $N = 20$  plots, one-tailed test, with Bonferroni correction due to regression to seven different hills), the total number of newly established colonies at the site ( $P = 0.023$ , Fig. 2b), and the number of queens at a site ( $P = 0.036$ , Fig. 2c). For all other hills, the one-tailed Bonferroni-corrected probabilities are  $P > 0.6$ .

Not only are all population parameters related to the distance from Hill 7, they show concordant relationships. Using the relationship between queen burrow density and distance from this hill, we estimated that the distance beyond which no queens are expected to arrive from Hill 7 to be 810 m. Using the relationship of new colonies as a function of distance from this hill, we estimated that the distance beyond which no new colonies are expected is 730 m. Using the relationship of established colony density (in 1992) as a function of distance from this hill, we estimated that the distance beyond which density falls to zero is 860 m. These distance estimates suggest that 730–860 m is the neighborhood radius that is relevant for *P. occidentalis* population structure. Of course, factors such as local wind conditions on the day of the flight will modify this estimate for queen density, but should not affect colony density or the density of new colonies.

Although the correlation of population parameters with the distance from Hill 7 is high, it may be coincidental. To determine whether this location is unusual (and biologically meaningful), we calculated the correlation between the colony density, the density of new colonies, the number of queen burrows, and the distance to 5041 locations ( $= 71^2$ ) on 20-m grid intervals in a  $1.4 \times 1.4$  km area surrounding the study site. This additional area includes many other hills, although none that are as tall as Hill 7. The size of the correlation

←

colonies in 1992; and (c) for all 92 plots on the entire study site, as a function of the number of established colonies in 1992. Overlapping points are indicated in this diagram by increasing numbers of spikes in the star.

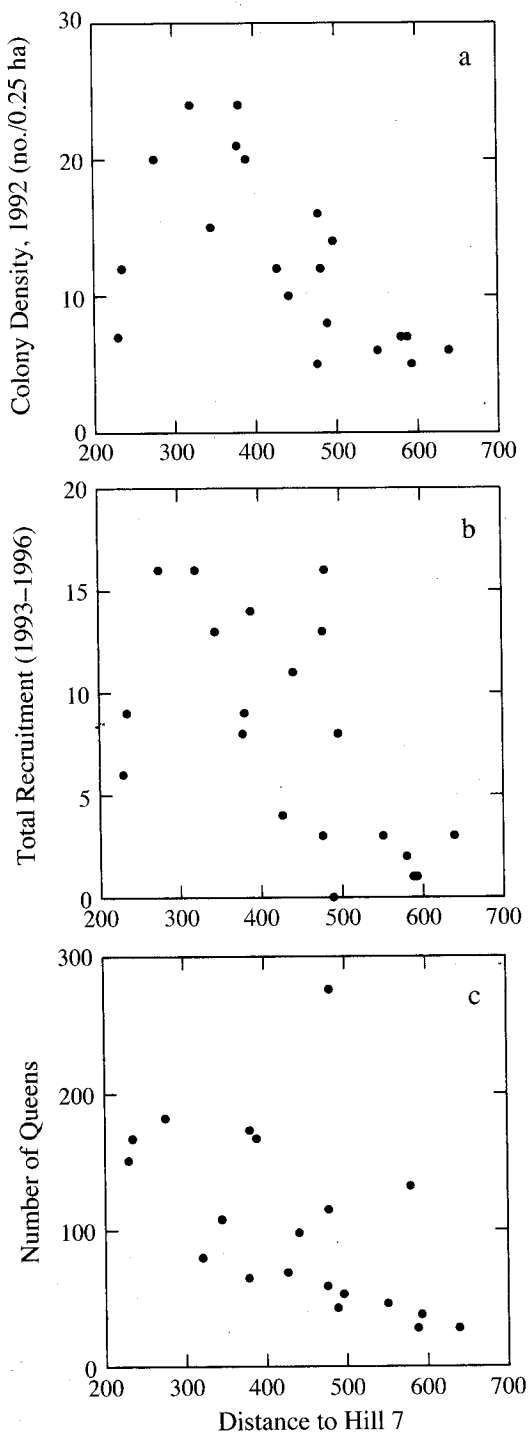


FIG. 2. Some properties of the *Pogonomyrmex occidentalis* study population as a function of distance to the largest hill at the study site: (a) colony density in 1992; (b) production of first-year colonies (1993-1996); (c) the number of queens landing on a plot (1996).

of the population parameter with distance to a location is color coded in Fig. 3. A single region shows the largest negative correlation with the established colonies (Fig. 3, top left), newly established colonies (Fig. 3, top right), and density of queens (Fig. 3, bottom left). The region that could have produced simultaneously highly significant correlations ( $P < 0.01$ ) for all population parameters is the relatively small area in Fig. 3, bottom right panel, that contains Hill 7.

The distance to Hill 7 has predictive value as well. Using the same methods we employed for selecting the initial 20 plots, we selected 20 additional plots from the study area and predicted the population density in 1992 and total recruitment from 1993 through 1997 using the known regression of initial density or recruitment on distance from the lek hill. The correlation of observed and predicted values was highly significant for both stages (total recruitment,  $r = 0.61$ ,  $P < 0.005$ ; initial density,  $r = 0.78$ ,  $P = 0.0001$ ).

Queen supplementation significantly increased the number of newly founded colonies (Wilcoxon matched-pairs signed-ranks test,  $P = 0.013$ , one-tailed). Five new colonies appeared on the control plots, while 17 new colonies were produced on the supplemented plots. With a total of 2700 queens added to the supplemented plots, and 12 additional colonies produced,  $p = 0.004$  was the overall average probability of successfully founding a colony. This figure may underestimate the probability of success because we did not know how many of the additional queens began nest burrows. For 1998, using the estimate of 42 additional queens per supplemented plot (or ~336 additional queens) we found that  $p = 0.015$  was the estimated success rate of queens in supplemented plots. (There were five additional colonies established on experimental plots relative to control plots in 1998.) This latter number was comparable to the natural success rate observed by Wiernasz and Cole (1995) and from the regression of new colonies on queen burrows reported above.

Because the supply of propagules (foundress queens) strongly influences population density in *P. occidentalis*, we predicted that there would be no overall relationship between measures of colony fitness and population density. As correlates of colony fitness, we used the plot-specific mortality rate, average colony size, and average colony growth for the 20 study plots. Density was not correlated with mortality ( $r = 0.15$ ,  $P > 0.25$ ,  $N = 20$  plots, all one-tailed tests), colony size ( $r = -0.10$ ,  $P > 0.2$ ,  $N = 20$  plots), or colony growth ( $r = -0.19$ ,  $P > 0.2$ ,  $N = 20$  plots). Neither was the distance to the tallest lek hill correlated with any of these measures: mortality ( $r = 0.09$ ,  $P > 0.5$ ,  $N = 20$  plots), colony size ( $r = -0.23$ ,  $P > 0.25$ ,  $N = 20$  plots), or growth ( $r = -0.11$ ,  $P > 0.5$ ,  $N = 20$  plots).

Based on the average colony lifetime of 17 yr, and the probability that a queen can found a colony ( $p = 0.013$ ), we estimated that 77 queens (an average of 4.52 queens per colony per year) must land on a plot to

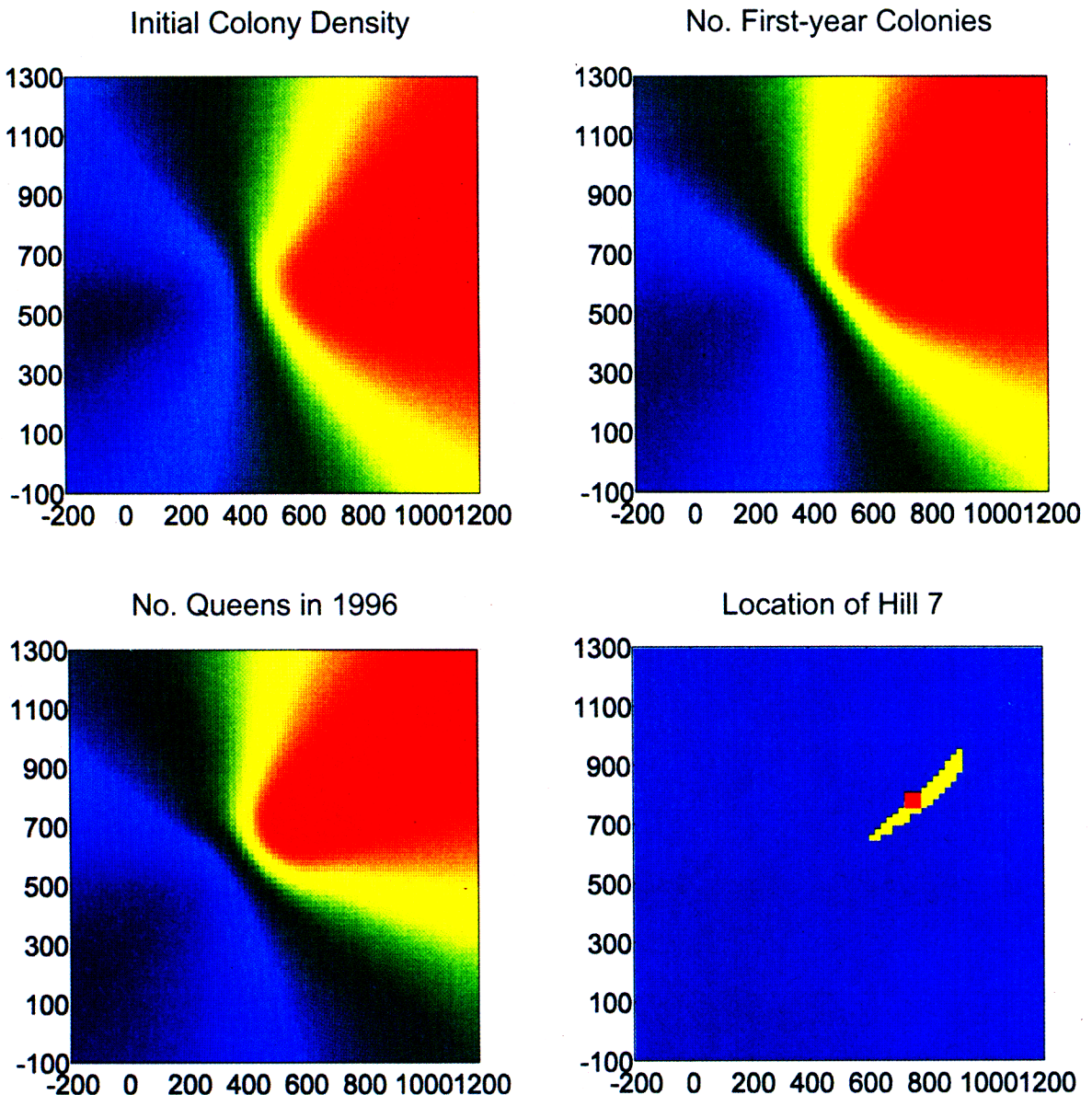


FIG. 3. The correlation between the distance between each location in a  $1.4 \times 1.4$  km area surrounding the study site and: (top left) the initial colony density (no./0.25 ha) in each of the 20 quadrats 1992; (top right) the number of first-year colonies produced during 1993–1996; and (bottom left) the number of queens in 1996. Correlation is coded from +0.5 (dark blue) to -0.6 (dark red). Each of the figures points to a region toward the east-northeastern portion of the study area as showing the highest correlation with the density of these life stages. (Bottom right) The region of the plot that shows simultaneously highly significant ( $P < 0.01$ ) correlation for all *Pogonomyrmex* life stages contains the tallest hill (shown as the red square symbol). Blue regions indicate locations for which correlations are not highly significant ( $P > 0.01$ ) for at least one population parameter.

replace each colony. The median density of propagules in 1996 was 89 queen burrows/plot. The average density of colonies in plots with more than the median level of propagules was 17.8 colonies/0.25 ha; we used this as the estimate of saturated density. To maintain this density, 81 queens per year must land on a 0.25-ha plot; plots receiving fewer propagules would not be saturated and may be limited by recruitment.

We tested whether we could predict the observed

density of colonies based on the availability of propagules. For unsaturated plots receiving  $<81$  propagules, there was a significant regression ( $P < 0.01$ ) of observed colony density (mean = 10.8 colonies) on the number of propagules (Fig. 4). The slope of this relationship ( $0.30 \pm 0.09$  colonies/propagule [mean  $\pm 1$  SE]) did not differ from the expected value of 0.22 ( $=pL$ ), and the y intercept ( $-4.53 \pm 4.8$ ) did not differ significantly from zero. On plots that received  $>81$



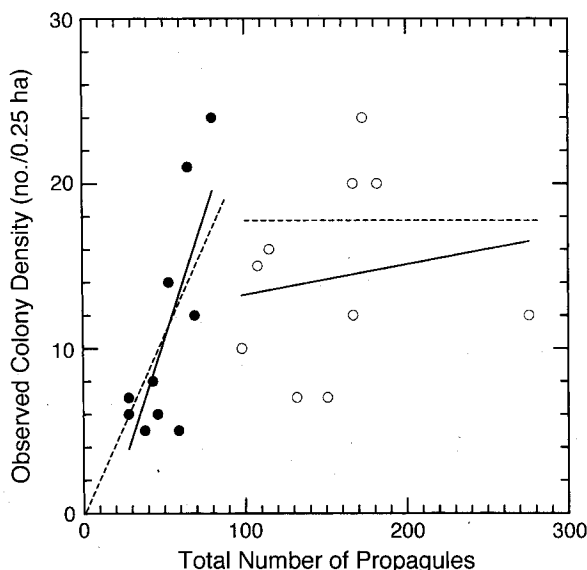


FIG. 4. The relation between colony density and propagule numbers. The solid circles are the plots classified as unsaturated; the hollow circles are plots classified as saturated. The solid lines are the regression of colony density on propagule number, while the dashed lines are the expected relations between the two quantities.

propagules, there was no relationship between the observed colony density and estimated colony density that would result (Fig. 4). The mean observed colony density was  $14.3 \pm 5.8$  colonies/0.25-ha plot, which did not differ significantly from the estimated value of 17.8 colonies per plot.

Although our data did not show density dependence when all plots are considered, we predicted that density dependence should be more apparent in plots that receive enough propagules to saturate density. We found a negative correlation between density and colony size ( $r = -0.63$ ,  $P = 0.026$ , one-tailed test); correlations between density and mortality ( $r = 0.28$ ,  $P > 0.2$ ) and density and growth ( $r = -0.22$ ,  $P > 0.25$ ,  $N$  for all = 10 plots), although in the expected direction, were not significant.

#### DISCUSSION

Our results are most simply explained as recruitment limitation: locations close to the site of the mating swarm are more easily reached by dispersing queens and have a higher local population density. The decline in foundress density with distance from the mating swarm is consistent with patterns of dispersal in other insect species (reviewed in Turchin 1998) as well as trees whose seeds are wind dispersed (Greene and Johnson 1989). Annual variation in food availability will affect the number of reproductives produced by individual colonies and consequently variation in the number of foundress queens. However, the large-scale, long-term pattern of population density should reflect the long-term average distribution of propagules in the landscape.

Habitat selection by queens may contribute to the pattern of foundress settlement. Queen distribution is highly clumped (B. J. Cole and D. C. Wiernasz, unpublished manuscript), suggesting that they actively select nest sites at the level of microsites. But in order for habitat selection to be solely responsible for the patterns of distribution, some as yet unquantified environmental feature must be a function of the distance to Hill 7, and dispersal itself must be independent of the distance to Hill 7. While we do not rule out habitat selection, limited dispersal from a single source is sufficient to explain the patterns we observe.

The spatial pattern of density is truly a landscape property that will be produced spontaneously by the interaction of queen movement and the attractiveness of hilltops for the formation of mating swarms. If sites vary in their attractiveness for mating, this will generate spatial pattern in density even if the initial density of colonies is completely uniform. More attractive sites for mating will be the foci for density increase. Increased density around attractive mating sites creates a positive feedback to produce spatial organization spontaneously. If the density of attractive sites is high, there may still be spatial variation in density as a function of recruitment limitation. Even if all places are near a suitable mating site, diffusive instabilities (Kareiva 1990:58–59) may spontaneously produce persistent spatial patterns. But if the distance between attractive sites is on the order of the dispersal distance, then density variation is easily produced on larger spatial scales. The pattern of abundance in this species may not be understandable without reference to the presence of subtle geographical features.

Overall population density is an outcome of processes that occur on a large number of local scales. Assuming that queens move the same distance when traveling to the mating swarm as when they disperse from the mating swarm, the distance over which the queens disperse to new nest sites (~800 m) determines the set of local neighborhoods that contribute to a single mating swarm. In some neighborhoods, density-dependent processes may occur, while others lack evidence of density dependence. In effect, the variation in local neighborhood density is erased when all of the queens disperse first to the lek site for mating, and then away from it for colony founding. This is a spatial version of the storage effect hypothesis (Chesson 1985) for a single species. The storage effect hypothesis suggests that temporal, particularly annual, variation in density due to variations in reproduction is damped by storage of propagules in something like a seed bank.

Studies of the importance of scale in ecology have often compared the evidence for density dependence (reviewed by Ray and Hastings 1996, Williams and Liebhold 2000), at local scales and at larger scales in a hierarchical analysis. Differences in the significance of local and higher scales of comparison have been often been observed. In immobile insect stages, evidence for density dependence



was found in 7–16% of studies at larger spatial scales, while 65–69% of studies showed density dependence at smaller spatial scales (Ray and Hastings 1996). We suggest that scale is important in a different way in this system. The relevant scale over which density dependence can operate is always local. Scale becomes important relative to the distance from a source of propagules. When the distance from the source is small enough to ensure that a local neighborhood is saturated in density, we see evidence of density dependence. Increasing the distance from the source of propagules reduces the evidence of density dependence. Scale is not used hierarchically, but as a way of establishing categories such as saturated vs. unsaturated plots. If a hierarchical analysis of scale was used in the present study, the evidence for density dependence would depend critically on the mixture of saturated and unsaturated local sites. In species where spatial variation in density is influenced by recruitment, hierarchical aggregation of local neighborhoods may be misleading.

This type of spatial analysis might be profitably applied to other systems. For example, habitat fragmentation or disturbance may produce edge habitats that contain populations with different demography (mortality and fecundity schedules). To determine the spatial scale of disturbance that influences the population ecology of the organism, one might compare demographic properties inside and outside a proposed disturbance scale or distance. When the scale of classification is appropriate to the scale of disturbance, one may observe shifts in demography.

Recruitment limitation has been widely reported in marine systems and may be of considerable importance to the population dynamics of some marine species (Caley et al. 1996). Limited recruitment also may explain the diversity of tropical and temperate forests (Schupp 1990, Alvarez-Buylla and Garcia-Barrios 1993, Hurtt and Pacala 1995, Hubbell et al. 1999). Species that display recruitment limitation share certain life history features: a highly dispersive stage, usually the juveniles, and a sedentary stage that decouples local recruitment from local reproduction. Because a number of terrestrial species, especially insects and plants, have these characteristics, recruitment limitation may be frequent in these systems.

Ants have been a paradigmatic example of species whose populations are limited by space and resource availability. Several studies have shown both intraspecific (De Vita 1979, Ryti and Case 1984, 1992, Gordon and Kulig 1996, Billick et al. 2001) and interspecific (Vepsäläinen and Pisarski 1982, Cole 1983) competition. The regularity of colony dispersion patterns is attributed to intense intraspecific competition (Levings and Traniello 1981, Ryti and Case 1986). Ants are among the most frequent examples of insect species that show strong competition for food resources (Davidson 1985). This study suggests that resource or scramble competition for food or space is not the fundamental factor determining pop-

ulation density in *P. occidentalis*. While there may be competition for space and/or food (Gordon and Kulig 1996, Billick et al. 2001), it acts secondarily on the distribution of foundresses generated by the spatial distribution of mating swarms.

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