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Recruitment in the harvester ant, *Pogonomyrmex occidentalis*: effects of experimental removal

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Abstract We examined the importance of experimental removal of mature colonies on colony recruitment in the western harvester ant *Pogonomyrmex occidentalis*. To test the common assumption that established colonies suppress the establishment of new colonies we removed all colonies in ten 0.25 ha plots in 1996 and an additional five plots in 1997 and measured new colony recruitment in 1997, 1998, and 1999. Using a blocked, paired plot design we found that removal of colonies increased new colony recruitment in some areas of the site, but not others. Spatial variation in the importance of established colonies to recruitment was consistent across years; blocks in which density dependence was important in one year exhibited density dependent recruitment in following years. We estimated that in the blocks where recruitment was affected by established colonies, they accounted for less than 10% of the mortality of foundress queens. The increase in the number of new recruits (on average two additional new colonies) was considerably less than the number of colonies removed; average colony density in the removal plots was 14 colonies per 0.25 ha plot. The consistent lack of importance of established colonies to recruitment in one block and the relatively small response to colony removal in the other blocks suggests that the number of new colonies in a year may not be equivalent to the number of deaths of established colonies in that year. Space limitation is an important influence on recruitment in *P. occidentalis*, but the magnitude of the limitation varies spatially.

Keywords Density dependence · Recruitment · *Pogonomyrmex* · Ants · Experimental removal

Introduction

The ecology of many ant species suggests that density should strongly affect recruitment and survival in populations and, therefore, indirectly affect population dynamics. Because ant species are commonly long-lived, are thought to saturate their environment, and are not herbivores, Hölldobler and Wilson (1990) argue that competition for space and/or resources is the main factor affecting local abundance of many ant species. Indeed, numerous behavioral observations support the importance of both intra-specific and inter-specific competition. Colonies of some species defend absolute territories (see Wilson 1971; Hölldobler and Lumsden 1980; Hölldobler and Wilson 1990 for reviews), and foraging columns of neighboring colonies often avoid each other (Hölldobler 1976; Harrison and Gentry 1981; Ryti and Case 1986; Gordon 1992). Additionally, colonies of some species engage in ritualized behavior to contest food (Hölldobler 1981; Ettershank and Ettershank 1982). Over-dispersion of nest sites is commonly cited as evidence of intra-specific competition (for a review see Levings and Traniello 1981), though such over-dispersion may result from other factors (Ryti and Case 1992). There is also evidence that greater size and number of neighbors reduces productivity (Gordon and Wagner 1997), the recruitment of colonies (Gordon and Kulig 1996), and survivorship of new colonies (Ryti and Case 1988a; Tschinkel 1993; Adams and Tschinkel 1995; Wiernasz and Cole 1995).

Although this observational evidence suggests that established colonies have a negative effect on the establishment of new colonies (e.g. Jerome et al 1998), there is little experimental evidence for this connection. Direct, experimental demonstration of intraspecific competition for food and/or space in ants is not common. Herbers (1986) demonstrated the importance of nest sites to the number of colony fragments in *Leptothorax longispinosus* and several studies (Pontin 1969; Ryti and Case 1988a) demonstrated increases in colony productivity when neighbors were removed. Very little is known, however, about the magnitude, the temporal consistency

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and spatial extent of the effect of mature colonies on new colony establishment. Without this information, we are unlikely to be able to understand the processes that produce variation in local density of a species.

Despite reasons to assume that successful recruitment in ant species is primarily determined by proximity to established colonies, other processes cannot be ignored. Ant populations of some species resemble some sessile marine species because they are "open" systems (sensu Roughgarden 1986). In these ant species queens mate in swarms, often well away from their colonies of origin. Spatial variation in patterns of queen dispersal may be just as important to local abundances as density dependent processes (Cole 1934; Wiernasz and Cole 1995; Cole and Wiernasz, unpublished data).

Pogonomyrmex occidentalis Cresson is a common harvester ant species in the western United States (Taber 1998). Colonies reach thousands of workers in size (Keeler 1993) and local densities of 80 colonies/hectare (personal observation). The high local abundance of *P. occidentalis* colonies suggests that competition might be particularly severe, but the swarm mating system of *P. occidentalis* suggests that its population dynamics might be governed by spatio-temporal variability in dispersal that overwhelms the effect of local density. Considerable work on harvester ants has documented a wide range of behavioral patterns consistent with density dependence (Hölldobler 1976; Harrison and Gentry 1981; Ryti and Case 1986; Gordon 1992), but we are aware of no experimental work linking colony densities to intraspecific density-dependent dynamics in any harvester ant species.

We tested the hypothesis that recruitment of new colonies is influenced by the presence of established *P. occidentalis* by removing all colonies of this species from 0.25 ha plots and measuring recruitment of 1-year-old colonies into the population. Colonies are extremely vulnerable in their first year. Because larger colonies can reduce future resource competition by killing queens, established colonies are suspected to be a major source of mortality to founding queens and their subsequent colonies. Workers of several species attack foreign queens, and established colonies of *P. occidentalis* often excavate conspecific and heterospecific queens as new queens excavate their burrows (personal observation). New colonies may suffer additional mortality because intense resource competition with neighbors reduces their ability to survive winter. Thus mature colony density is commonly negatively correlated with colony establishment in harvester ant species (Ryti and Case 1988b; Wiernasz and Cole 1995; Gordon and Kulig 1996).

Sites differ in local population density by as much as an order of magnitude (Wiernasz and Cole 1995), so we considered it likely that there was considerable variation in site characteristics. Sites may vary qualitatively, either in some measure of habitat suitability (e.g. food availability or soil characteristics), or in their proximity to sources of propagules. To test whether removal of established colonies influenced recruitment, independent of these site characteristics, we compared the effects of colony removal in sites from different locations and densities.

Materials and methods

The 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 1,470 m elevation. The soil is alkaline clay with seleniferous patches and is dominated by saltbrush (primarily *Atriplex gardneri*, *A. confertifolia* and *A. corrugata*), greasewood (*Sarcobatus vermiculatus*) (all Chenopodiaceae), and *Xylorhiza venusta* (Asteraceae). The common herbaceous species are *Oryzopsis hymenoides*, *Hilaria jamesii* and *Anisthane tectorum* (all Poaceae), and several species of crucifers (Brassicaceae).

P. occidentalis queens and males form mating swarms on unusually high points in the landscape following rain in late summer. The location of these swarms is largely consistent from one year to the next, though swarms do not form at all locations every year. Upon dispersing from the swarm, single queens initiate colonies that may live 45 years (Keeler 1993). Queens forage during the initial stages of colony initiation until the eclosion of the first brood.

Ten pairs of 50×50 m square plots were laid out in 1996 and, to increase statistical power, an additional five pairs of plots were added in 1997. We initially surveyed many hills in the area; most of the hills selected in 1996 were the site of mating swarms in that year. A pair of 0.25 ha plots was laid out at the base of each hill. Plots were laid out in a block design with five hills within each block to control for a strong spatial component to recruitment (Wiernasz and Cole 1995). Within blocks, each pair of plots was matched based on location (pairs were generally within 20 m of each other), vegetation, and colony density. Plots were all located in relatively flat areas. The distance between any two pairs within a block was generally within half a kilometer, though one pair of plots in block A was approximately 4 km from the other pairs. Blocks were approximately 1–3 km apart. In each pair of plots, one member was arbitrarily assigned to the removal treatment, the other was a control. Because we cannot be certain what environmental variables might be important to density determination and to colony establishment (e.g. soil or vegetation characteristics, presence of other ant species), we assigned plots to treatments arbitrarily and analyzed all data by pairing a specific control to a removal plot.

All *P. occidentalis* colonies within each removal plot and a 10-m buffer zone around the plot were killed by placing one to three tablespoons of Amdro next to the nest entrance in the morning as foraging began. We removed any excess poison that remained in the late morning or early afternoon after foraging stopped. Colonies were checked 1–2 weeks later to ensure they were dead, and repoisoned and checked again if live workers were still present. A second poison treatment invariably killed the colony. We killed colonies in the 10-m buffer zone because workers from colonies outside the plot were not prevented from foraging within the removal plots. Average intercolony distances on the plots before removal were of the order of 15 m, and consequently we assumed that a buffer zone of 10 m should have been sufficient to dramatically, if not completely, reduce foraging by outside colonies. Foraging ranges of colonies neighboring the buffer zone may have increased, as found in *P. barbatus* (Gordon 1992). However, based on approximately 40 h of qualitative observation within the removal plots following colony removal, there was little foraging by colonies from outside the plots. Thus, we conclude that the buffer zone was of sufficient size to adequately reduce the impact of colonies neighboring the buffering zone to detect a treatment effect.

Plots were surveyed in June and July of 1997, 1998, and 1999 and the number of old and first year colonies were counted. In each removal plot, we again killed any colonies of *P. occidentalis* that were present in the removal plots. These new colonies consisted both of new colonies as well as occasional older colonies that moved into the plot or buffer zone from the outside. We tagged mature colonies in the control plots in the 1997 and 1998 censuses in order to reduce the number of second year or older colonies mistaken for first year colonies during the 1998 and 1999 censuses. Although we did not tag colonies in the control plots in 1996, the effect of this was to bias recruitment upwards in control plots, because second and third year colonies that are growing slowly will be similar in size, and potentially confused with, first year colonies. The results we report for 1997 are therefore conservative. In the 1997 census we distinguished new colonies from older colonies primarily by colony size.

We used analysis of covariance to analyze the data. We used the square-root transformation on the number of new colonies to normalize the residuals. Treatment and block were included as fixed effects and pairs of plots were nested within blocks. Because we could not completely eliminate differences in density between members of a pair of plots, we included initial density of colonies in each plot as a covariate. Block effects were treated as fixed effects because we were interested in hypotheses explaining patterns of spatial autocorrelation. We analyzed data from the 3 years separately because 10 of the 30 plots were not present in 1997, rendering repeated measures analysis of variance problematic.

Results

There were originally 11.4±3 (mean±SD) colonies per plot (see Table 1 for data summary) before colony removal. Blocks differed considerably in average original colony density (block A: 9.9±1.6 (mean±1 SD); block B: 10±2.5; block C: 14±3.1, $F_{2,\ 27}$=10.2, P<0.001) with block C having colony densities somewhat greater than previously reported at other locations on the site (Wiernasz and Cole 1995). The effect of removal also varied considerably among blocks; removal increased recruitment on average 1 recruit/plot per year in block A and 3.1 recruits/plot per year in blocks B and C.

Table 1 A summary of the results from colony removal experiments. The numbers are the total recruits per block for control and removal plots in the 3 years of the study. Block C was added to the study in 1997

	1997	1998	1999
Block A			
Control	14	10	2
Removal	8	4	3
Block B			
Control	6	2	5
Removal	20	13	13
Block C			
Control	–	5	6
Removal	–	14	17

There was a strong spatial component to recruitment; recruitment was positively correlated within plots between years when the data were analyzed using a Pearson correlation with a stepwise Bonferroni correction (1997 and 1998: R=0.56, P<0.05, n=20; 1998 and 1999: R=0.50, P<0.05, n=30; 1997 and 1999: R=0.37, P=0.10, n=20). Removing colonies increased colony recruitment, although the effect of removal varied spatially and temporally. The results of the ANOVA are given in Table 2. There was a treatment by block interaction in all years. Colony removal did not have much of an effect on colony recruitment in block A, while recruitment increased considerably in removal plots in blocks B and C (Fig. 1). In 1998 and 1999 there was also a significant treatment effect: removal of established colonies increased recruitment. The difference between 1997 and 1998–1999 is probably due to the increase in the number of blocks after 1997. The number of new colonies varied between years (1997: 2.4±1.7 (mean±1 SD); 1998: 1.6±1.4; 1999: 1.5±1.4). The consistency of our results (e.g. the presence of a block by treatment interaction in all three years) eliminated the necessity of combining data across years in order to increase the power to detect a treatment effect. This allowed us to avoid the problem of the missing block in 1997 in a repeated measures analysis.

Discussion

These results provide mixed support for the common conception that competition for space and/or food drives spatial patterns of abundance in long-lived, numerically dominant ant colonies. Removal of established colonies

Table 2 Anova table for the effects of ant removal (treatment) on colony recruitment

Year	Effect	*SS*	*df*	*MS*	*F*-ratio	*P*
1997	Treatment	0.234	1	0.234	0.976	0.356
	Block	0.063	1	0.063	0.262	0.625
	Density	0.050	1	0.050	0.207	0.663
	Treatment × Block	1.883	1	1.883	7.841	0.027
	Plots within blocks	2.167	8	0.271	1.128	0.444
	Error	1.081	7	0.240		
1998	Treatment	0.636	1	0.636	6.244	0.030
	Block	0.002	2	0.001	0.011	0.989
	Density	0.041	1	0.041	0.403	0.538
	Treatment × Block	2.635	2	1.318	12.932	0.001
	Plots within blocks	1.760	12	0.147	1.440	0.277
	Error	1.121	11	0.102		
1999	Treatment	1.430	1	1.430	15.005	0.003
	Block	1.431	2	0.715	7.504	0.009
	Density	1.040	1	1.040	10.915	0.007
	Treatment × Block	0.861	2	0.430	4.514	0.037
	Plots within blocks	1.825	12	0.152	1.595	0.224
	Error	1.049	11	0.095		

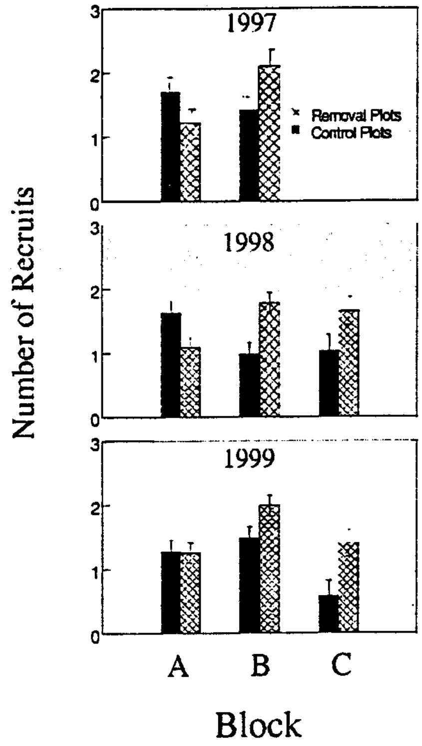

Fig. 1 The Block × Treatment effect on colony recruitment in 3 years. The number of new recruits is the least-squared estimate of recruitment after removing the plot, block, treatment and density main effects. We use the term recruits to refer to colonies established by foundress queens in the previous year

significantly increased recruitment, independent of variation in density or location in 2 of the 3 years of the experiment. However, the most consistent result was the Treatment × Block interaction effect. Blocks differed consistently in how they responded to the effects of experimental removal. Two of the blocks (B and C) showed the expected pattern, where removal of mature colonies increased recruitment. However, in one of the blocks (A), recruitment has tended to be lower in plots with mature colonies removed (Fig. 1).

The finding of density dependence in some blocks supports previous work on harvester ants. In this species, distance from established colonies affected survivorship of colonies 1 year old and older (Wiernasz and Cole 1995). Additionally, new colonies of *P. barbatus* tend to occur away from established colonies (Gordon and Kulig 1996). The mechanism underlying the effect of established colonies on colony recruitment is unclear. Foragers will kill queens above the ground and occasionally they will even excavate queens from their burrows (personal observations). Colonies may also lose foragers in encounters with neighboring colonies (De Vita 1979). Additionally, new colonies may also be vulnerable to resource limitation and lack the reserves to survive through winter. Thus, removal of established colonies may have indirectly affected colony establishment.

In the blocks B and C where removing colonies had an effect, we can estimate the effect established colonies had on recruitment. Removing colonies increased the number of recruits from one colony per plot per year to three colonies per plot per year. Survivorship of foundress queens through the first year of colony life is about 1.3% (Wiernasz and Cole 1995, Cole and Wiernasz, unpublished data). If removing established colonies did not change the number of queens that arrived at a site, then survivorship was increased to about 4%. Consequently, factors independent of established colony density were responsible for over 90% of the mortality of foundress queens.

This estimate of the importance of older colonies to new colony establishment is based on removal of all colonies on the removal plots. It seems likely that the rate of first year colony establishment monotonically increases as the percentage of all colonies removed within plots increases. There is the possibility, however, that the relationship between new colony establishment and the percentage of colonies removed is nonlinear and that removal of a lower percentage (less than 100%) of colonies might have generated higher rates of recruitment and consequently higher estimates of the importance of density dependence. Such a relationship could result if the presence of older colonies reduces the density of predator species.

Removal of adult colonies may increase short-term survivorship higher than our estimates of 4%, but higher recruitment rates may be obscured if increased new colony density lowers ultimate survivorship. Because foundress queens in *P. occidentalis* are active above ground for several weeks after colonies are initiated, aggressive interactions among queens could reduce survival and lower density of recruits. Survivorship of colonies in their first year is negatively correlated with increasing density of foundresses (Wiernasz and Cole, unpublished data). Thus, density of foundress queens, rather than density of adult colonies, may also be more important in determining adult colony densities. With these factors in mind we conclude that although there was density dependence attributable to adult colonies in some locations, density independent factors or density dependent mortality associated with other first year colonies accounted for a large portion of new colony mortality.

While mature colony density consistently reduced new colony recruitment in blocks B and C, removal had no effect on recruitment in block A. The cause of this block by treatment interaction is unclear. There is considerable spatial heterogeneity in the distribution of foundress queens across the study site. Both the number of queens arriving at a site and the subsequent number of first-year colonies are correlated with the density of established colonies (Cole and Wiernasz, unpublished data). Block A had the lowest original colony density and so it probably had the lowest number of arriving queens. Consequently the absence of new queens arriving at plots in block A may have been more important to the rate of colony recruitment than density dependent effects. Spatial variation in the survivorship of queens and their subsequent colonies could also generate the block by treatment interaction. With the current data, we cannot determine which factor was more important for generating the block by treatment interaction.

The block by treatment interaction was not an artifact of spatial variability in the effectiveness of our removal treatment. One potential explanation for the block by treatment interaction is that the removal of colonies was not as effective in block A, where recruitment was higher in the control plots than the plots with colonies removed. We reject this possibility because colony density is strongly spatially autocorrelated (as indicated by the block effect on colony density and other unpublished results) and original colony density was lowest in block A. Consequently, the number of colonies bordering plots was lowest in block A. Thus, if anything, our removal treatment was probably most effective in low density areas, like block A; the same location where removing mature colonies did not increase recruitment. Consequently, the block by treatment interaction is not an artifact of spatial variability in the effectiveness of our treatments in any obvious manner.

Thus, our findings demonstrate that regions have site specific patterns of new colony establishment. The effect of removing colonies was largely consistent within blocks across years, and recruitment was significantly correlated within plots across years. Consequently there was a consistent spatial component to patterns of new colony recruitment and the effects of mature colonies on recruitment. Our results on new colony establishment run counter to findings for *Pogonomyrmex barbatus*, where location has no effect on the mortality of adult colonies (Gordon and Kulig 1998). Gordon and Kulig's (1998) was done on a smaller spatial scale and focused on interactions among neighboring colonies. Thus, our results indicate that on a larger scale, the importance of neighborhood effects of established colonies varies spatially and suggests that either colony survivorship or rates of queen arrival in an area must be sufficiently high for established colonies to have any noticeable effect on colony recruitment.

Inferences from terrestrial systems suggest that the long-lived, sessile, numerically dominant nature of harvester ant colonies should be associated with strong density dependent effects on recruitment (Schoener 1983; Hölldobler and Wilson 1990). Along these lines ants are commonly characterized as being resource and space limited with strong intraspecific competition (e.g. Hölldobler and Wilson 1990). Findings that older and larger colonies are largely unaffected by intraspecific competition (Gordon and Kulig 1998), in conjunction with empirical evidence that older colonies affect new colony establishment (Ryti and Case 1988b; Wiernasz and Cole 1995; Gordon and Kulig 1996), have led to the comparison of ant population dynamics with those of gap dynamics in trees (Wiernasz and Cole 1995; Gordon and Kulig 1998). A new colony needs the death of an old colony to open a "gap" and allow successful recruitment (Hölldobler 1981; Ryti and Case 1992). Our results suggest that, at least for *P. occidentalis*, population dynamics are more complicated. Not only did removal of colonies fail to affect recruitment in one block, the increase in recruitment in the other blocks failed to match the number of colonies which were removed. While the removal of established colonies increased the number of new colonies by one to two colonies, original colony density averaged 11.4 (3.2 SD) per 0.25 ha. Thus colony recruitment is not equivalent to the number of gaps opened up by mortality of established colonies. A local population would require at least 4–5 years of increased recruitment before the number of colonies could return to pre-removal levels.

The framework of strong space limitation with recruitment being driven by adult mortality has also been commonly applied in sessile marine communities (Dayton 1971; Connell and Slayter 1977; Lubchenco and Menge 1978; Sousa 1979; Gaines and Lubchenco 1982). Roughgarden et al (1985), however, have argued that gap dynamics will not always drive the population dynamics of such systems. If the rate of settlement into such systems is too low there will always be some free space and the importance of density dependence to establishment of new individuals will be relatively diminished. A similar dynamic may be acting in this population of *P. occidentalis*.

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