

Overdispersion of ant colonies: a test of hypotheses

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Summary. The nest locations of two ant species in the Colorado Desert are intraspecifically overdispersed. Intraspecific overdispersion has been thought to represent strong intraspecific competition. Here we consider this hypothesis along with three competing hypotheses: microhabitat selection by foundress queens, predation on foundress queens, and predation on established colonies. To test these hypotheses five types of data were collected: (1) the forager population sizes of *Veromessor pergandei* and *Pogonomyrmex californicus*, (2) the response of the territory use of *V. pergandei* to varying levels of food, (3) the encounter rates of conspecifics and other ant species to foundress queens artificially placed near and far from conspecific colonies, (4) predation on colonies as a function of colony spacing, and (5) the relationship between the plant microhabitat at the nest and colony spacing. The results show that established colonies have no apparent selectivity for a particular type of plant microhabitat nor do foundress queens show avoidance or attraction toward conspecifics. *V. pergandei* workers show only a slight ability to find *V. pergandei* queens that are artificially placed near their entrances. Certain spiders are the most common ant predators on our study area. Direct observations on spiders indicate that colonies with closer neighbors are not prone to a higher risk of predation. In addition, the estimates of the death rate of workers from a mark-recapture technique indicate that colonies with closer neighbors lose similar numbers of workers as compared to colonies with further neighbors. In favor of the competition hypothesis, the summed size of intraspecific nearest neighbor pairs are larger for colonies that are spaced further apart than those colonies that are spaced closer together. We also develop an index of foraging directionality for the column foraging species *V. pergandei*. Using this measure, we find that nearest neighbors tend to avoid foraging toward each other. The response of territory use to food levels was tested with experiments involving patches of cracked wheat. These experiments showed that patches away from nearest neighbors were found significantly sooner than patches toward nearest neighbors. The above five sets of data together suggest that resource competition and perhaps queen predation by established colonies account for the intraspecific spatial patterns of these species.

The regular arrangement (overdispersion) of sessile animals, plants, or nest locations is often attributed to competition acting between and/or within species (Bray 1956; Woodell et al. 1969; Elmes 1974; Yeaton and Cody 1976; DeVita 1979; Harrison and Gentry 1981). Typically overdispersion is demonstrated by comparing the mean observed nearest neighbor distance with the expected nearest neighbor distance generated from some random distribution. To date no study has tested whether alternate hypotheses could explain the observed spatial patterns equally well.

Here we consider two intraspecifically overdispersed ant species (Ryti and Case 1984) and four hypotheses that might produce their spatial arrangement. 1) Intraspecific competition. Inter-colony competition could effect colony spacing patterns by promoting extinction of interstitial colonies when food space or some other resource is limiting. 2) Predation on foundress queens. Predation by established conspecifics on nearby foundresses could produce overdispersion. 3) Predation on established colonies. Predators on these ants may forage frequently on closer colonies, causing tightly packed colonies to go extinct. 4) Microhabitat preferences of foundress queens. Suitable nest sites (some species-specific set of soil and vegetation characteristics) might be overdispersed.

We examine the foraging dynamics and the forager population sizes of two seed harvesting ant species, estimate predation rates and study certain aspects of microhabitat preferences to determine which of the four mechanisms produce the observed pattern of overdispersion.

Methods

The study was conducted from April, 1981 through April, 1985 within the Philip L. Boyd Deep Canyon Desert Research Center, a part of the University of California Natural Reserve System. The study site was a 3 ha area of alluvial fan habitat at an elevation of 300 m.

We examined the nest locations of two of the most conspicuous ant species, *Veromessor pergandei* and *Pogonomyrmex californicus* to determine their spatial associations. The taxonomy of these species is based on Wheeler and Wheeler (1973). *V. pergandei* is a seed harvester ant with mostly non-overlapping foraging territories that forages using columns of workers. These columns are typically 10 to 30 m long and the ants fan out to exploit a patch of resources

over the last third of the trail. *P. californicus* is a harvester ant that forages individually with little or no interaction with members of the colony. Members of this species will, however, congregate and form trails to artificially rich resource patches (pers. obs.). The nest locations of the two species were determined, and intraspecific nearest neighbor (closest conspecific colony) distances were calculated using the methods of Clark and Evans (1954). The study site was periodically checked to make sure all colonies had been located. Although nest relocations of *P. californicus* are common at some sites (DeVita 1979), such behavior was not observed at our study site. We checked the border areas of the site to ensure that the nearest neighbor for each colony had been found, thus the corrections to the Clark and Evans method suggested by Sinclair (1985) were not necessary.

Five types of observations were made to test which of the alternate hypotheses affect the spatial arrangement of these species. The resulting data included (1) colony sizes of *V. pergandei* and *P. californicus*, (2) response of territory use of *V. pergandei* to varying levels of food, (3) encounter rates of conspecifics and other ant species to foundress queens seeded near and far from conspecific colonies, (4) predator preferences and death rate of colonies as a function of spatial packing, and (5) relationship between the plant microhabitat near the nest and colony spacing.

Population estimates

The foraging population was estimated using a simple mark-recapture technique. Ants were individually marked on the dorsal surface of the gaster with a drop of diluted Testor's enamel model paint after they were immobilized by exposure to carbon dioxide (dry ice). The marking apparently had no effect on the interactions of the marked individuals with other unmarked members of the colony. For *V. pergandei* colonies, between 100 and 300 workers were marked from each colony and released. Then the next day we observed between 500 to 1,000 workers returning along the foraging trail at a point about one meter from the nest entrance, noting the proportion that was marked. A multiple mark-release-recapture experiment was performed over two days to show that the marked and unmarked foragers were mixing randomly within the colony and that there was no excess mortality caused by the marking procedure. This was done by comparing the number of marked individuals from the first and second days that were observed foraging on the third day with what was expected from random mixing. Foraging population size was calculated using the Lincoln index. For the *P. californicus* colonies censused a similar protocol was followed with the exception that 20 to 80 foragers were marked and between 20 and 100 workers carrying food items were censused the next day to get the proportion marked.

We also tested the effect of the mark on mortality with *P. californicus* using 20 marked and 20 sham-marked workers. After 10 days in the lab, which was longer than the usual observation period, one marked worker was dead and one unmarked worker was dead. Thus, marking did not cause any excess mortality.

As an indication that competition is important to colonies once they are established, we examined the effect of nearest neighbor distance on the forager population size. This is an analogous procedure to one used in plant studies

to demonstrate competition. In plant studies, the summed size of both individuals in a nearest neighbor pair is regressed against the corresponding nearest neighbor distance (Pielou 1960). If neighboring colonies compete for shared resource, then we expect those nearest neighbor pairs that are relatively close together to be smaller than those that are far apart.

Territory use observations

The foraging behavior of *V. pergandei* was investigated in more detail. From April to September 1981 the direction and length of the foraging trail was measured whenever a colony was active. These data indicate the extent to which an ant colony utilizes its territory (see below). *V. pergandei* colonies are active all year around, confining their harvesting activities to the night and early morning hours during the summer. We censused each active colony about once per hour. To estimate the foraging activity of the colonies, the return rate of workers per minute on the foraging trail was measured one meter from the nest entrance. Since the return rate is a function of substrate temperature (Gordon 1978), we used only data collected during the maximum activity period of each day. We used the maximum return rate data to determine whether ant activity is correlated with the nearest neighbor distance or the foraging trail length.

To determine whether colonies were avoiding foraging toward neighbors, we calculated a relative territory utilization (RTU) index. This index was based on the foraging trail direction relative to the direction of a colony's intraspecific neighbors. A colony's "neighbors" are those colonies that have bordering territories. These territories are mostly non-overlapping, although neighboring colonies occasionally forage on the same patch. Thus neighbors are those colonies that can potentially forage on adjacent patches. The "nearest neighbor" is the colony that is closest. RTU(A,B) is the territory use of colony A relative to neighboring colony B.

$$RTU(A, B) = \frac{1}{mn} \sum_{j=1}^m \sum_{i=1}^n [\cos(b_i - a)] \frac{L_i}{L_{\max}}$$

where:

- b_i = foraging direction of colony A on day i ,
- a = direction of colony B measured from colony A,
- L_i = column length of colony A on day i ,
- L_{\max} = maximum column length of colony A during each observation period,
- n = number of days that both colony A and colony B were active during any observation period,
- m = number of observation periods.

The RTU (A and B) = [RTU(A,B) + RTU(B,A)]/2. This combined RTU index ranges between 1 and -1. A RTU of -1 would indicate that the two colonies always forage directly away from each other whereas a RTU of 1 would imply that the two colonies always forage directly toward one another. Random territory use (with random trail lengths) by both neighbors would make the index zero. We devised this index to be a measure of the chance of neighbor interactions, and that is the reason that the trail length is included in the calculation of the index. We expect that if a colony's foraging direction is independent of its neighbors, then, on average half of the colony pairs will

have positive RTU indices and half will be negative. The RTU index was averaged for all neighbors during each observation period in 1981 to get an estimate of overall territory use.

We tested the effect of resources and neighbor location on the foraging behavior of *V. pergandei* with two types of cracked wheat experiments. In the first set of experiments, performed in September 1983, 200 gm of cracked wheat were uniformly spread over a 10 m² patch halfway between four pairs of nearest neighbors. In the second experiment, performed in July 1984, we placed 100 gm of cracked wheat in a uniform density 5 m² patch in a direction away from the nearest conspecific neighbor (RTU < 0). If possible, the patch was also placed so that it was not toward the second nearest conspecific neighbor. The patch was the same distance from the colonies in both experiments. Six of the eight colonies from the first experiment were used in the second experiment.

Queen settlement and predation

We observed *V. pergandei* queen settlement during the February 1983 mating season. The species of the nearest established colony was noted. We also noted the occurrence of foundresses near a third ant species, *Myrmecocystus flaviceps*, because it is highly predaceous. We included this ant species to see if foundresses would avoid potential predators. To estimate potential predation rates, *V. pergandei* foundress queens were placed in 50 ml plastic vials and were buried upright and flush with the soil surface 3 m from conspecific established colonies and 3 m from *P. californicus* colonies (and at least 10 m from the nearest *V. pergandei* colony). A 5 mm hole was bored into the cap to allow crawling insects to enter and a layer of Tanglefoot was applied to the top 2–3 cm of the inside of the vial to prevent crawling insects from escaping. We placed some cotton soaked with 5 ml of water at the bottom of the vial to provide a water source for the dealated queen. These experiments will only test for one type of detection of queens (olfactory) and perhaps other cues are necessary for workers to detect queens. Because of the low mating activity at our study site in 1984 and 1985 we collected female alates and foundress queens at the south side of South Mountain Park, Phoenix, Arizona in March 1985. The female alates were made to shed their wings by cold stress. Stress-induced queens also lay eggs and become negatively geotropic (S.W. Rissing pers. comm.). A total of 20 stress-induced queens and 20 foundress queens were used in these experiments. Half of each group was placed near *V. pergandei* colonies while the other half was placed near *P. californicus* colonies. The vials were buried so that their caps were flush with the surface. After the vials containing the queens were collected, new vials without queens were placed in the same locations to serve as controls. The vials were checked for ants and other insects after 5 and 10 days.

Predation estimates

The predation rate was estimated through the total loss rate of workers. *Pogonomyrmex californicus* workers from twenty colonies were marked using the same protocol as before (at least 30 workers at each colony were marked). We censused the proportion of ants marked for four to eight days (until the mark was rare). Marked ants were assumed to be lost at a constant proportion per day. To

estimate the number of ants lost per day, the loss rate was multiplied by the number of ants in the colony.

The notable potential predators of these ants are horned lizards, spiders and more uncommonly mammalian predators (such as coyotes) that may excavate entire nests (Parks 1929; Chew 1979). Horned lizards and spiders both tend to ambush the ants. Due to the rarity of horned lizards (after extensive searches only 4 were seen in three years time and only one recapture over one week from the initial sighting) and absence of mammalian predation on the colonies, we studied the effects of spiders on colonies as a function of neighbor distance. The occurrence of three species of spiders (*Steatoda* sp., Theridiidae; *Pellenus* sp., Salticidae; *Euryotis* sp., Theridiidae) at *P. californicus* colonies was noted directly during July and August 1984. *P. californicus* colonies were then put into one of two categories; those with spiders and those without spiders. These spiders were typically observed foraging on ants within 50 cm of the nest entrance.

Microhabitat preferences

We assessed the microhabitat preferences of mature colonies by measuring the density and type of perennials around the nests of *V. pergandei* colonies. The density of perennial plants could have a major impact on the temperature and humidity in the nest itself. Thus plants are used an indicator of the preferred microhabitat.

The preference of foundress queens was used as a measure of microhabitat requirements. These measurements were made on *V. pergandei* foundresses after the February 1983 mating season. If microhabitat requirements are the most important factors governing spatial arrangement, then foundresses should occur most frequently close to established conspecific colonies.

Results

Spatial patterns

The nest sites of *V. pergandei* and *P. californicus* when compared intraspecifically are significantly further apart than would be expected if nest locations were random (Table 1). The Clark and Evans (1954) nearest neighbor method has recently been criticized (Burgess, Ralston and Shaw 1982 and Sinclair 1985) especially for sample sizes of less than 100. However, the Monte Carlo random colonization simulations of Ryti and Case (1984) confirmed that the species studied here were overdispersed.

Table 1. Intraspecific spatial association for two desert ant species. $E(r)$ is the expected nearest neighbor distance if the colonies were randomly located. C is the standard variate of the normal curve, and p is the probability of the standard variate being the large. $E(r)$, the standard variate, and the index of aggregation were calculated using the method of Clark and Evans (1954)

Species	Mean nearest neighbor distance (m) (st. dev.)	N	$E(r)$ (m)	C	p
<i>V. pergandei</i>	18.2 (4.60)	22	14.1	2.64	<0.01
<i>P. californicus</i>	16.0 (6.81)	29	12.3	3.15	<0.002

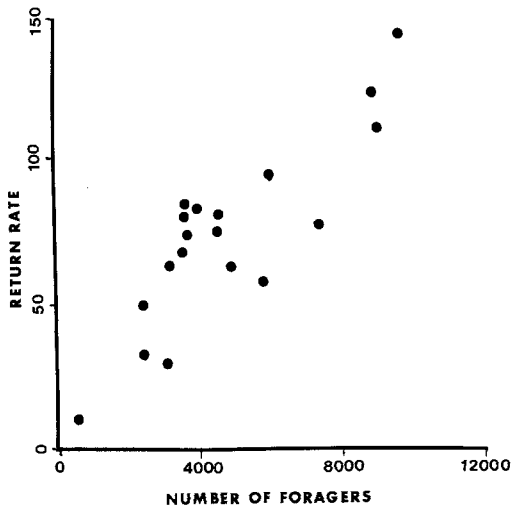


Fig. 1. Plot of the average return rate versus the number of foragers as estimated by a mark-recapture technique for 22 *V. pergandei* colonies. The correlation of these two variables is 0.835 ($P < 0.01$)

Population densities

The trail activity measurements provided some interesting correlations. For example, the return rate is strongly correlated with the mark-recapture population size estimates (Fig. 1) ($r = 0.835$, $n = 22$, $P < 0.01$). The return rate data and the mark-recapture estimates of colony size both indicate that the *V. pergandei* colonies differ in size. Since the return rate data could be measured more frequently, we used the mean return rate as a relative measure of the forager population size.

The colony sizes of both species followed the prediction of the competition hypothesis. That is, we found a significant positive correlation between the nearest neighbor distance and our estimate of total colony size, the summed mean return rate for each nearest-neighbor pair ($r = 0.708$, $P < 0.01$) (Fig. 2). A similar pattern was observed for 20 *P. californicus* colonies. There was a significant correlation of individual colony size and nearest neighbor distance ($r = 0.561$, $P = 0.01$) (Fig. 3). Thus, large colonies tend to be relatively far apart from one another as compared to smaller colonies. This relationship indicates that spatial dispersion affects a contemporary measure of fitness.

Territory use observations

One way of looking at territory use is to compute the average RTU index for an entire season. During 1981, 27 pairs of *V. pergandei* neighboring colonies showed a strong tendency toward avoidance of interaction between neighbors. The null hypothesis predicts that equal numbers of colonies have positive and negative combined RTU indices, however, only 8 of 27 pairs of colonies are observed to have positive combined RTU indices ($P = 0.0522$; based on a two-tailed binomial distribution.) The pairs of colonies can be divided into 12 nearest neighbor pairs and 15 non-nearest neighbor pairs. For the nearest neighbor pairs, the combined RTU index for one of 12 pairs is positive ($P = 0.0064$). On the other hand, the set of non-nearest neighbors has seven of its 15 pairs greater than zero, which is indistinguishable from chance. Thus, nearest neighbors tend to forage in opposing directions as compared either to a null

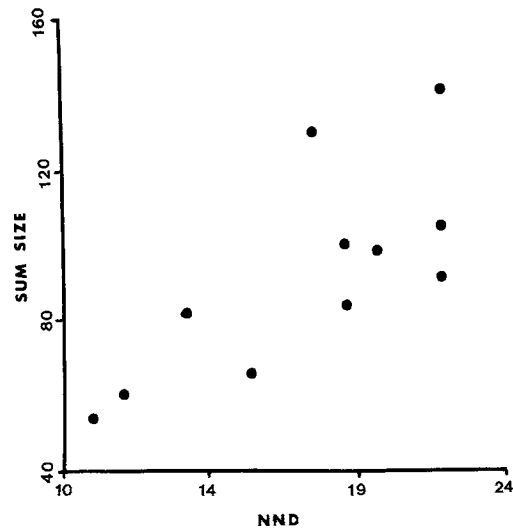


Fig. 2. Plot of the sum average return rate for nearest neighbors of *V. pergandei* colonies versus the nearest neighbor distance. The correlation of these two variables is 0.708 ($n = 12$ nearest neighbor pairs, $P < 0.01$)

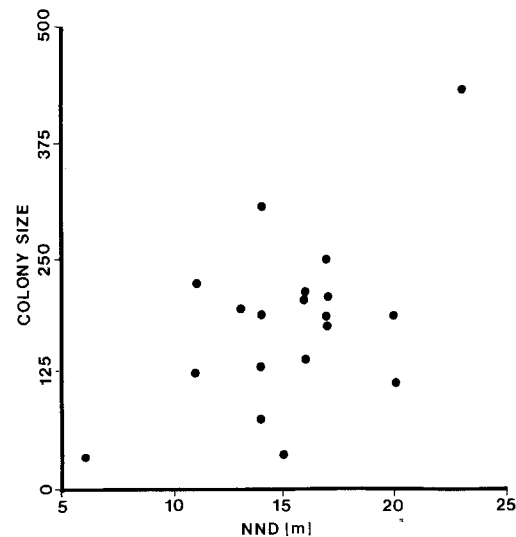


Fig. 3. Plot of colony size versus nearest neighbor distance for 20 *P. californicus* colonies ($r = 0.561$, $P = 0.01$)

model or as compared to non-nearest neighbors. Neither subgroup nor the entire set of colonies exhibit a significant correlation of RTU with the distance between neighbors.

The above data relating territory use and neighbor location show some trends, and they may indicate that resources are not ordinarily abundant enough between nearest neighbors to offset the potential cost of territorial "wars". We tested the response of *V. pergandei* foraging behavior with two sets of cracked wheat experiments: 1) a patch of cracked wheat was placed directly between pairs of nearest neighbors; and 2) a patch of wheat was placed away from the nearest conspecific neighbor. Patches toward nearest neighbors were foraged, on average, two days later in the experiment than patches away from all neighbors. The two distributions of colonies foraging on the patch (Fig. 4A, B) were compared with a Mann-Whitney U test ($W = 1065.5$, $P < 0.001$; toward nearest neighbor group: medi-

Table 2. Summary of the characteristics of *P. californicus* colonies with or without spiders feeding on them. None of the variables are significantly different (tested with ANOVA)

	Spider occurrence				F
	Present		Absent		
	N	mean (st. dev.)	N	mean (st. dev.)	
Colony size	11	188.0 (85.3)	17	144.1 (88.9)	1.67
NND	12	16.5 (5.23)	18	17.5 (4.53)	0.31
Loss rate (number/day)	5	20.7 (15.3)	4	15.2 (11.2)	0.36

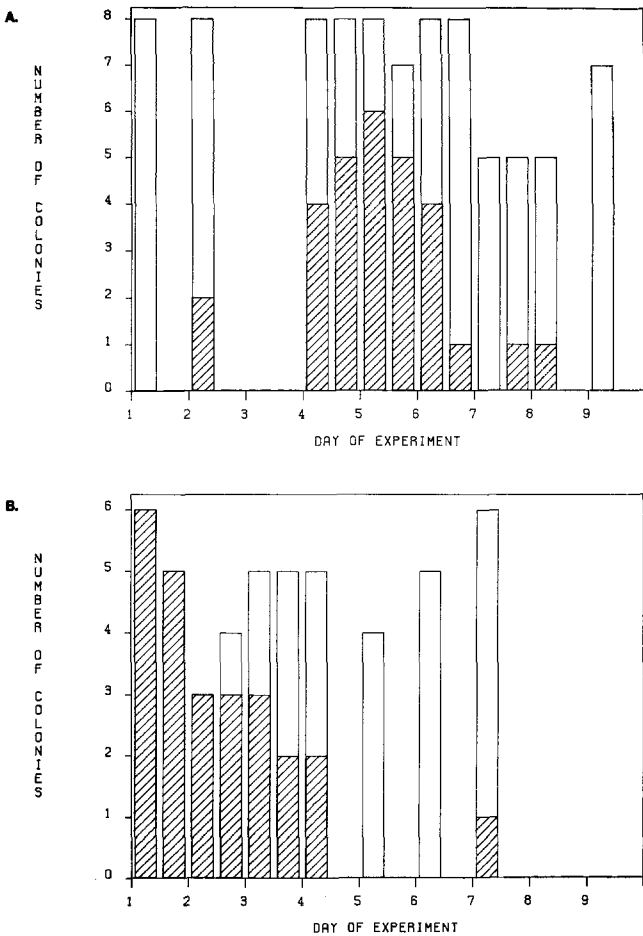


Fig. 4 A, B. Summary of the cracked wheat experiments. The open bar indicates the number of colonies active and the hatched portion shows the number of colonies that are foraging on the patch of cracked wheat. The bars for each day represent the AM and PM foraging sessions. **A** The patch of cracked wheat was placed directly between four pairs of nearest neighbors. (note it rained on day three and the colonies were not active). **B** The patch of wheat was placed away from all neighbors of six colonies. These two distributions were compared with a Mann-Whitney U test ($W = 1065.5, P < 0.001$)

an = 4 days, $n = 29$; away from all neighbors group: median = 2 days, $n = 25$). The results of these experiments are striking in two respects: 1) they show that either type of experimental patch is foraged upon until it is gone; 2) that the patches away from all neighbors are found during the

Table 3. Summary of the nearest neighbor of *V. pergandei* foundress queen nests. The expected number is based on the observed frequencies of established nests of those three species. The total chi-square is 2.25 ($P > 0.05$)

Nearest neighbor	Number of foundresses	
	Observed	Expected
<i>V. pergandei</i>	9	9.6
<i>P. californicus</i>	9	12.7
<i>M. flaviceps</i>	20	15.7

Table 4. Summary of the encounter rate experiments using *V. pergandei* queens seeded 3 m from *V. pergandei* colonies (a) and seeded 3 m from *P. californicus* colonies (b). The vials were checked for spiders and ants after 5 and 10 days. The first set of values in each table represent the fraction of vials with either spiders or ants, and the values in parentheses show the occurrence of ants in the vials

		Found	Not found	Chi-square	
(a) 5 days	Queen	5 (5)	15 (15)	6.46** (3.75)	
	Control	13 (11)	7 (9)		
	10 days	Queen	6 (5)	14 (15)	12.38*** (6.46)**
		Control	17 (13)	3 (7)	
(b) 5 days	Queen	2 (2)	18 (18)	2.50 (0.78)	
	Control	6 (4)	14 (16)		
	10 days	Queen	6 (5)	14 (15)	3.64 (0.48)
		Control	12 (7)	8 (13)	

first foraging session, while the patches toward nearest neighbors are not found for at least one day after they are first available to the colonies (Fig. 4).

Foundress queen settlement and predation

Foundress queens settle randomly with respect to the species identity of the nearest established colony (Table 3). The encounter rate experiments indicated only a slightly higher occurrence of *V. pergandei* workers in the vials containing the queen (2 of 20 vials near *V. pergandei* colonies) as opposed to the controls (1 of 20 vials near *V. pergandei* colonies). However, the two queen vials had a total of 10 *V. pergandei* workers while the control vial contained only a single worker. This may indicate that *V. pergandei* are attracted to the vials to a small degree by the presence of the *V. pergandei* queen. This is not true of other ant species or spiders. In fact, the proportion of vials containing either spiders and/or ants was higher for the controls than for the queen vials (Table 4). When comparing the controls and the vials containing queens, the occurrence of all ant species was more similar between the two sets than was the combined occurrence of ants and spiders (Table 4). These data indicate that spiders and non-conspicuous ants are not attracted by the smell of foundress queens.

Predation estimates

The impact of predation on colony spacing was measured indirectly through death rate and directly by observing the

occurrence of spiders at colonies. The expectation is that predators forage more on closely-spaced colonies. A mark-recapture study on 20 *P. californicus* colonies showed no such trend; closer colonies tended to lose about the same number of workers per day as did colonies with more distant nearest neighbors. The correlation of ant loss rates and the nearest neighbor distance was only $r=0.363$ ($P < 0.20$). The preferences of the spiders also did not conform to the expectation of the predation hypothesis (Table 2). There is no significant difference in the nearest neighbor distance of colonies with spiders versus those without spiders. Spiders do apparently have an effect on the prey colonies, since colonies with spiders lose 36% more workers per day than colonies without spiders. Moreover, spiders do show some preference for larger colonies, and this preference probably explains the slight positive correlation between the number of ants lost and nearest neighbor distance.

Microhabitat preferences

The plant microhabitat around *V. pergandei* colonies is quite variable, there is a tendency for colonies with small territories to have more plants within their territories ($r=0.471$, $n=20$, $P < 0.05$). Foundress queens, observed in February 1983, showed no selectivity for the species identity of their nearest neighbor (Table 3). For microhabitat selection to be a cause of overdispersion the suitable nest sites have to be filled, otherwise the nearest neighbor distance would decrease. If foundress selectivity indicates the preferred microhabitat, then such sites are probably not all taken since conspecifics were neither preferred nor avoided as nearest neighbors. If any generalizations can be made regarding the habitat preferences of *V. pergandei* nests, it is that their entrances rarely open up under a perennial plant. This preference hardly constrains their choice since 82.2% of the space is not covered by perennials.

Discussion

Colony spacing

Intraspecifically the nest locations of *V. pergandei* and *P. californicus* are overdispersed and interspecifically the nests are aggregated (Table 1, Ryti and Case 1984). However, a survey of the ant literature reveals that intraspecific nearest neighbor distances are not always greater than interspecific nearest neighbor distances. For example, Elmes (1974) compared the spatial patterns of two ant species in a limestone grassland. One species was aggregated and the other species was randomly distributed.

The ant territorial system is an extremely dynamic one: selectivity of foundress queens, colony expulsion, and nest relocations allow fine tuning of the spatial arrangements. DeVita (1979), who studied *P. californicus*, also found the nests to be overdispersed. Moreover, he demonstrated the importance of relocations of established nests by observing that most relocations increased the nearest neighbor distance. Competition with a nearest neighbor may not always be the proximal cause for nest relocations. Artificial shading of colonies has been found to increase the proportion of colonies that relocate by more than five fold for colonies of *P. badius* (Carlson and Gentry 1973). *P. badius* occurs in open old fields in the Southeastern United States. Nest

relocations did not affect the nearest neighbor distance of *P. badius*, which also has been found to have overdispersed colonies (Harrison and Gentry 1981). Regardless of the proximal cause of relocation, it allows for continual adjustment of the spatial relationships between colonies beyond any generated by queen settlement.

Population estimates

The mark-recapture technique has been tested before to determine its accuracy in estimating the actual population size. DeBruin et al. (1977) found a significant correlation between the estimates generated by the Lincoln index and the actual colony size as determined by excavation of the nest. Although mark-recapture is not a reliable estimate of the actual size of the colony (Erickson 1972), it does provide a good *relative* estimate of colony size. Some studies have indicated that the foraging population is a set percentage of the total colony size (Porter and Jorgensen 1981). We found the return rate of *V. pergandei* foragers to be highly correlated with the number of foragers. Since the colony size is probably not constant during the course of a year, we used the average return rate as the long term average of colony size.

An indication that competition is important between colonies of the same species is that the sum of the population sizes of nearest neighbors increases for more distant neighbors. This phenomenon has been previously shown for perennial plants in the Mojave Desert (Yeaton 1978; Yeaton and Cody 1976). A confounding effect on such expectations is that resources are not uniformly distributed. Colonies with smaller territories and closer neighbors tend to have higher densities of resources (more plants). Thus intraspecific competition may be mollified to some degree for closer colonies since they have more resources with which to coexist. More importantly, it shows that resource density is heterogeneous and that ant colonies tend to be denser in resource "hot spots".

Effect of resources on foraging behavior

We found that *V. pergandei* nearest neighbors as a whole are somewhat more likely to forage on the same patch of resources when resources are more abundant. The pair of cracked wheat experiments demonstrated that resource concentration has a significant effect on foraging behavior. Nearest neighbors will forage on the same patch if it is rich enough, but there is a time lag in finding a rich patch if it is toward a colony's nearest neighbor.

Effects of conspecifics on foraging behavior

Territory utilization in *V. pergandei* is affected by neighboring colonies. This result has also been observed in other species. The trunk trails of the Florida harvester ant, *P. badius*, are affected by the location of the colony's neighbors (Harrison and Gentry 1981). If the trails were extended, they would not intersect the nests of any of their neighbors. Holldobler (1981) studied *Myrmecocystus mimicus*, which defend spatiotemporal territories. He found that neighboring colonies sometimes engage in complex display tournaments, which create a kind of dominance order. But often there were no aggressive interactions between the colonies; instead, neighboring colonies would forage in direc-

tions that did not bring them into contact with foragers from other *M. mimicus* colonies. It is easy to envision similar behavior in a fixed territorial species, such as *V. pergandei*.

Foundress queens and colony spacing

For queen settlement to be a viable mechanism to account for the observed colony spacing, queens must avoid founding colonies near conspecifics and tend to aggregate near other species. This is certainly not the case for *V. pergandei* queens. However, there is some evidence that *M. mimicus* queens do select uninhabited sites more often than sites near established colonies (Bartz and Holldobler 1982). Some have suggested that the observed intraspecific territorial patterns in ants are regulated by the expulsion (predation) of foundress queens within a colony's foraging area and the expelling of entire colonies that are too close to an established colony (see Holldobler 1979 for review). Holldobler (1981) concluded that queens of *M. mimicus* would not succeed within 3 m of an established nest, and that queens founding colonies within 3 to 15 m of established colonies would run a high risk of expulsion. The encounter rate experiments presented here did not give such dramatic results, but these experiments only mimic the initial response to foundress queens. It is reasonable to expect that the new colonies are at a competitive disadvantage to established colonies (in terms of a territorial fight) for at least one year after founding. Thus, observations need to be made on the response of established colonies to foundress colonies over a longer period of time.

Predation and spacing of colonies

The usual effect of predation on ant colonies has been a change in the prey's foraging schedule rather than an effect of predation on the nest location (Gentry 1974; Whitford and Bryant 1979; Schaffer and Whitford 1981). However, there is some evidence suggesting that large mammals, such as coyotes, may excavate honey ant colonies (Parks 1929 and Chew 1979). The effect of predators need not be so dramatic to be a cause of overdispersion. Predators need only prey more often on more tightly packed colonies. Both spiders (Holldobler 1970) and horned lizards (Rissing 1981) are known to be important predators of harvester ants. However, no one has previously examined the effect of predation rates on colony spacing.

Neither the death rate data nor the spider occurrence data we collected support the notion that predators prey more on closely packed colonies. In fact, the nearest neighbor distances of preferred and non-preferred colonies are statistically indistinguishable. In view of these data there is little evidence for these predators having an impact on the spacing of these ant colonies. We should also note that horned lizards include a very low proportion of *V. pergandei* workers in their diet and a high proportion of *P. californicus* workers (Rissing 1981). If horned lizards were important contributors to colony spacing patterns, then the effect would be lower on *V. pergandei* than on *P. californicus*. Yet both species have a similar degree of overdispersion on our site. Moreover, if the spacing of *P. californicus* is only an historical remnant of the effects of past horned lizard predation, then we expect that the forager population size of *P. californicus* colonies should be randomly related

to nearest neighbor distance. But the positive correlation of forager population size and nearest neighbor distance indicates that spacing currently affects the fitness of colonies.

Microhabitat of the nest

We used the density of perennial plants above the nest as a measure of microhabitat since they could be censused reliably. A myriad of other variables (temperature, soil characteristics or humidity) could also have been measured. Some of these may be important cues to the queen founding her nest and some may not be as important. The characteristics of the plants above the nests of *V. pergandei* indicate no special requirements for a particular plant species or density of plants. The only observation of importance is that colonies rarely have their nest entrances under perennials. Open space, though, is not limited, since it comprises 82.2% of our study site. An even more telling observation concerns the sites that queens chose to found their nests. These foundresses showed neither avoidance nor attraction toward established conspecific nests, indicating that more potential nest sites are still available and that microsite is not the most important factor in colony spacing. The spatial arrangement of *V. pergandei* at Boulder City, Nevada provides an interesting contrast to that at our site. The Nevada site has a discontinuous *V. pergandei* distribution (S.W. Rissing pers. comm.). Some areas are apparently too steep and rocky for *V. pergandei* to found colonies. However, in suitable areas where colonies do occur the nearest neighbor distance (about 18 m) is nearly the same at both sites (S.W. Rissing pers. comm.). This indicates that microhabitat is important, yet where *V. pergandei* occurs the spacing pattern is the same. Thus, microhabitat preferences are not a sufficient explanation of ant spacing patterns.

In conclusion, intraspecific competition between adults and expulsion (predation) of foundress colonies are important causes of overdispersion while the supporting evidence for the role of queen settlement, predation, and microhabitat preferences in the spacing of the colonies is weak or absent. This assertion is supported by five lines of evidence. These are: (1) the nest sites of foundress queens are distributed randomly with respect to neighbor identity, (2) *V. pergandei* workers show a slight ability to find nearby foundress queens, (3) tightly spatially packed colonies do not suffer from more intense spider predation, (4) the summed size of close colonies is larger than for more distant colonies, and (5) the territory use of colonies is affected by both the resource level and the presence of neighbors. However, long-term manipulative experiments (addition of resources and removal of colonies) need to be performed to make a conclusive argument. Such experiments are currently in progress on *V. pergandei* and *P. californicus*. Additional experiments are currently in progress to test the response of established colonies to foundress colonies in their territories.

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