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Spatial arrangement and diet overlap between colonies of desert ants

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Summary. The spatial patterns and diets of three desert ant species were examined. The results indicate that food competition may account for the spatial arrangement of these species, and that only intraspecific interactions may be required. Each ant species was significantly overdispersed, and the average intraspecific nearest neighbor distances were greater than the interspecific nearest neighbor distances. A test of pairwise spatial arrangment showed that all three species pairs were aggregated interspecifically. The level of the interspecific aggregation was related to the diet similarity of the species. The two species pairs with the lowest diet overlaps were significantly aggregated, and the species pair with the most similar diets was not significantly aggregated. Pairwise dietary overlaps between colonies showed that average intraspecific overlaps were significantly greater than interspecific diet overlaps. Furthermore, the diet overlap was significantly positively correlated to the mean nearest neighbor distance for the three intraspecific and three interspecific comparisons. These data indicate competition for food, especially within species, may be regulating the intercolony distances of these ant species. A computer simulation tested whether only intraspecific territoriality is necessary to produce the observed nearest neighbor distances. A simulation that placed colonies randomly on a patch confirmed that these colonies are intraspecifically overdispersed. By adding intraspecific territoriality, the simulation nearest neighbor distances fit the empirical data reasonably well. Thus interspecific competitive interactions seem unnecessary to account for the spatial arrangement of these species.

Introduction

One readily measured pattern in natural communities involves the average distance between sessile individuals of one or more species. Whether inter- or intraspecific nearest neighbor distances are the larger is often used as evidence to assess the importance of intra- and interspecific competition (Bray 1956, Yeaton and Cody 1976, Elmes 1974). The assumption is made that sessile individuals become widely separated because they are avoiding one another or because competition has already eliminated interstitial individuals.

For species with similar carrying capacities to coexist, simple competition models predict that competition must be more intense intraspecifically than interspecifically. Although this condition is neither strictly necessary nor sufficient when more than 2 species are involved, it is usually the case that when intraspecific effects are relatively strong compared to interspecific effects, coexistence between all species becomes more likely (Strobeck 1973, Gilpin 1975, May 1974). When the distance between sessile individuals is related to the amount of potential competition between them, intraspecific nearest neighbor distances should be larger than interspecific nearest neighbor distances. Here we examine the spatial arrangement of the colonies of three desert ant species to determine if the observed intercolony distances are in line with this prediction. Secondly, we ask if the diet overlaps between conspecific colonies are generally greater than diet overlaps between colonies of different species, and if among different species pairs, diet overlap increases as nearest neighbor distance increases. To the extent food resources are limiting, these diet overlaps will be indicative of the level of competition. Finally, we ask whether intraspecific territoriality is sufficient to explain the observed spatial patterns of ant colonies or whether we must invoke interspecific territoriality as well.

Methods

The study was conducted from April, 1981 through September, 1982 within the Philip L. Boyd Deep Canyon Desert Research Center, a part of the University of California Natural Land and Water Reserves System. The study site was 1.74 ha. of alluvial fan habitat at an elevation of 300 m. The study site was homogeneous in plant composition and soil type.

We determined the nest locations of three conspicuous ant species, *Veromessor pergandei, Pogonomyrmex californicus*, and *Myrmecocystus flaviceps*. The study site was checked periodically to ensure that all nests had been located. There was no apparent turnover of nests during the study. The microhabitat nest site preferences of these species are apparently similar. Only *V. pergandei* has multiple nest entrances, of which one is usually used at any one time. Here the colony location was taken as the average of all nest entrances seen during the study. *V. pergandei* is a seed harvester ant that forages using columns of workers to exploit patches of resources. *P. californicus* is also a harvester ant; however, its workers forage individually. The third species, *M. flaviceps*, a honey ant, is highly predaceous, and exhibits little cooperation between foragers. *M. flaviceps* primarily feeds on insects, but also feeds on extrafloral nectaries and nectar (Wheeler and Wheeler

1973). These species all overlap temporally in their foraging. From the nest locations, we calculated the intraspecific and interspecific nearest neighbor distances. The "nearest neighbor" is the closest colony, either a conspecific or a non-conspecific, depending on the comparison. The nearest neighbor need not have been within the study site. The intraspecific spatial patterns were analyzed using the technique of Clark and Evans (1954). We used Pielou's (1961) test to determine the interspecific spatial patterns. This analysis uses the frequency of nearest neighbors measured from each species in a two species comparison. The statistic generated by this analysis is the index of segregation, which ranges from −1 to 1. It is negative when nests are interspecifically aggregated, zero when spatial patterns are generated by a Poisson process, and positive when nests are intraspecifically aggregated. Because there is usually a large proportion of reciprocal nearest neighbor pairs, the ordinary significance levels for a chi-square contingency table analysis cannot be used (Meagher and Burdick 1980). To obtain the expected ditribution for chi-square analysis, simulations were performed that maintained the spatial arrangement of the colonies, but which randomly assigned species identity (using the method of Meagher and Burdick 1980).

Food items were collected from foragers of twelve colonies for each species. Food was collected so as to give approximately equal sampling effort in terms of the proportion of the foraging population sampled. Thus 100 items were collected from *V. pergandei* colonies while only 40 items were collected from the smaller *P. californicus* and *M. flaviceps* colonies. Food items were divided into 33 categories as follows: grass seeds, grass blades, *Cryptantha* sp. stems, other stems, creosote seeds, *Peucephyllum schottii* seeds, other composite seeds, *Cryptantha* sp., seeds capsules, other seeds, *Hyptis emoryi* flowers, *P. schottii* flowers, other flowers, leaves, other plant parts, rock, feces, *V. pergandei* workers, *P. californicus* workers, *M. flaviceps* workers, *Solonopsis* sp. workers, other ants, other hymenopterans, coleopterans, homopterans, hemipterans, dipterans, othopterans, lepidopteran larvae, other lepidopterans, termites, other insects, arachnids, and lizard skin. The diet overlap between each of the 36 colonies was calculated using symmetrical and asymmetrical versions of the formula of Pianka (1974). The individual colony overlaps were pooled into three interspecific and three intraspecific groups and compared using the method of Huey et al. (1983). This analysis uses simulations that randomly assign species identity to colonies keeping the number of colonies of each species constant. For the 24 colonies of each two species diet comparison there are a total of 576 different permutations. To estimate the significance levels, 200 permutations were randomly chosen and the mean interspecific and intraspecific diet overlaps were calculated. The distribution of the difference between the interspecific and intraspecific diet overlaps from these simulations was then compared with the empirical results. The self-overlap terms for each colony (by definition set to 1.0) were excluded from the analysis. Two points should be made regarding the number of food items censused per colony, since the low number of food items per category should skew the diet overlap estimates downward. First, this bias will affect all pairwise comparisons, and if the intraspecific overlaps are higher as we expect, then the interspecific and intraspecific diets will become more similar (not less). Second, when we use these data to compare various specific pairs we pool data across 12 colonies for each species. Thus our accuracy increases by that factor.

A computer simulation tested whether any interspecific interactions are necessary to explain the observed spatial patterns. The computer simulation placed colonies on a sphere having a surface area of one hectare at the empirically observed densities of 13 *V. pergandei* colonies, 17 *P. californicus* colonies, and 21 *M. flaviceps* colonies. The simulation was *not* intended to determine which factors were important in regulating colony density, but instead to test for spatial interactions given the observed densities. A sphere, rather than a square was used in the simulation to eliminate edge effects. Positions on the sphere were chosen by randomly selecting an altitude and azimuth. The value for the altitude was then corrected to give a uniform density on points on the sphere. Points were thrown down sequentially, thus simulating the colonization of an initially depauperate area. The simulation was first run with non-exclusive home ranges (non-interactive simulation) and secondly with exclusive intraspecific territories (interactive simulation). The simulations let us directly compare the intra- vs. interspecific nearest neighbor distances, since it takes into account the possible non-independence of these distances. In the interactive simulation, a nest location was discarded if it was within the territorial radius of an existing colony of the same species; a new random location was then chosen until it was outside the exclusive distance of all colonies of its species. This protocol mimics the sequential random colonizations of foundress queens and their subsequent expulsion if they land within some defended territory of existing colonies. Holldobler (1981) found that the colonization success of a foundress queen was highly dependent on her distance from an established colony. For *M. mimicus*, he found that a foundress queen had a small probability of successful colonization when it was within 15 m of an established colony. The radius of exclusion for each species was estimated by trial-and-error as the radius that yielded the closest match to the observed intraspecific nearest neighbor distance: 12.56 m for *V. pergandei*, 11.18 m for *P. californicus*, and 13.24 m for *M. flaviceps*. These values are reasonably close to the minimum observed nearest neighbor distances of 11 m for *V. pergandei*, 8 m for *P. californicus*, and 9 m for *M. flaviceps*, but are not expected to be exact since the defended area against invading queens need not be the same size as the foraging territory. Each simulation was run 40 times, and the average of the means of the nearest neighbor distances were calculated.

Results and discussion

The intraspecific nearest neighbor distances are greater than the interspecific nearest neighbor distances (Table 1). Recall that ordinary statistical comparisons of interspecific and intraspecific nearest neighbor distributions cannot be made because these distances are not independent and the sample sizes are not equal. For this reason we performed the non-interactive colony placement simulation and the results of this will be discussed below. Also, all three species are significantly overdispersed intraspecifically and two of the three two-species comparisons are significantly aggregated (Table 1, Table 2), a result consistent with the usual conditions for coexistence predicted from competition models.

The amount of diet overlap between colonies is a measure of the level of exploitation competition between colo-

Table 1. Mean nearest neighbor distances (±1 S.D.) for three desert ant species, *V. pergandei* (V), *P. californicus* (P), and *M. flaviceps* (M), measured to each of the three ant species. Sample sizes are in parentheses. Intraspecific nearest neighbor distances are greater than interspecific nearest neighbor distances, which is consistent with the predictions of simple competition models. Using the analysis of Clark and Evans (1954), each species was found to be significantly overdispersed intraspecifically

		To neighbor species		
		V	P	M
Measured from	V	18.2±4.60* (22)	11.9±8.07 (21)	8.71±5.47 (26)
	P	12.7±8.67 (29)	16.0±6.81** (29)	9.12±6.68 (29)
	M	14.2±7.49 (36)	12.3±9.59 (34)	16.5 ±6.30*** (36)

* $P<0.01$, ** $P<0.002$, *** $P<0.0001$

Table 2. Summary of the three two species spatial patterns as measured by the analysis of Pielou (1961) for three desert ant species *V. pergandei* (V), *P. californicus* (P), and *M. flaviceps* (M). Pielou's analysis usses the frequencies of colonies that are nearest neighbors to each species in the comparison. Significance levels were derived by simulations using the method of Meagher and Burdick (1980)

Comparison	S	Total Chi-square	*P*
V-P	−0.255	3.67	0.146
V-M	−0.586	18.12	<0.002
P-M	−0.613	21.49	<0.002

Table 3. Diet overlaps (mean±1 S.D.) for three desert ant species *V. pergandei* (V), *P. californicus* (P), and *M. flaviceps* (M). Twelve colonies of each species were sampled during July–September 1982. The average overlap for each intra- or interspecific comparison is taken over all appropriate colony pairs. The interspecific overlaps on each row were compared with the intraspecific overlap. Food overlap is significantly greater within each species than between species. (Note – significance levels from simulations, see text for details)

	V	P	M
V	0.518±0.268	0.419±0.216*	0.002±0.007**
P	0.419±0.216**	0.618±0.169	0.078±0.074**
M	0.002±0.007**	0.078±0.074**	0.620±0.199

* $P<0.01$, ** $P<0.005$

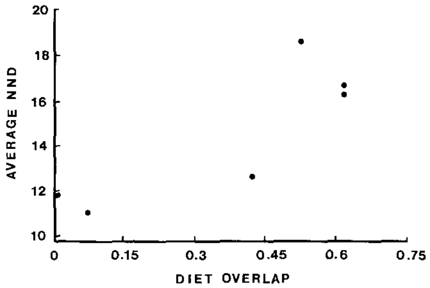

Fig. 1. Plot of the average nearest neighbor distance between and within species versus the diet overlap for that comparison for three desert ant species. The distance between ant colonies is apparently set by the amount of diet overlap between them. The correlation between average nearest neighbor distance and the diet overlap is 0.843 ($P<0.05$)

Table 4. Summary of standard variates of empirical nearest neighbor distances from computer simulation values for each comparison of three desert ant species. (*V. pergandei* (V), *P. californicus* (P), and *M. falviceps* (M). The standard variate was computed by subtracting the empirical distance from the simulation distance divided by the standard deviation of the means from the simulation. The top value in each cell compares the empirical data with that generated by a simulation that includes no intraspecific or interspecific interactions. The bottom value in each cell compares the empirical distance with distances generated by a simulation that includes intraspecific exclusionary territories. Only the intraspecific comparisons of the non-interactive simulation are significantly different from the empirical data

	V	P	M
V	2.00* −0.131	0.129 0.934	−1.35 −0.510
P	0.723 1.25	2.16* −0.022	−1.20 −0.287
M	0.308 1.53	0.298 1.88	3.67** 0.449

* $P<0.05$, ** $P<0.0002$

nies when resources are limiting. The primary foraging strategy of these ants is the collection and storage of either seeds or honey. This suggests that resources are not always abundant. Droughts can also stifle resource production (Tevis 1958), and are not uncommon in the area of our study site. Thus it is likely that the amount of diet overlap is indicative of the amount of competition. Since the asymmetric and symmetric overlap values gave qualitatively similar results, we will present only the symmetric diet overlaps. As determined by our Monte Carlo simulations, the intraspecific diet overlaps are significantly greater than the interspecific diet overlaps (Table 3). Furthermore, the average diet overlap values for the six pairwise species combinations are significantly positively correlated with the corresponding mean nearest neighbor distance (Fig. 1). This positive relationship occurs in spite of an inherent bias in the opposite direction. If resources are distributed heterogeneously and workers have no food preferences, then those colonies that are closer together should display greater diet overlap than colonies further apart. Instead we observe the opposite result, suggesting that the distance between colonies may be regulated by the amount of competition between them.

The non-interactive simulation supported the Clark and Evans (1954) test, and thus confirms the conclusion that the ant species are intraspecifically overdispersed. The empirical nearest neighbor distances were significantly larger than the non-interactive simulation values (Table 4). There was, however, no significant difference between the empirical and simulation interspecific nearest neighbor distances in the non-interactive model.

Recall that the size of the exclusive territories was set to be that which yielded a correspondence between the empirical intraspecific nearest neighbor distances and those produced by the simulation (Table 4). However, there was no consistent effect of adding intraspecific exclusive territories on the match between predicted and observed interspecific nearest neighbor distances. Adjusting the intraspecific nearest neighbor distances overall created a good fit to the empirical data (Table 3), since no simulation distance was significantly different from the relevant empirical nearest neighbor distance.

In the light of the results of the simulations we can now examine the results of the Pielou test. All three two-species comparisons were interspecifically aggregated, and the level of the association was related to the diet overlap between the species. The two harvester ant species were aggregated, but not significantly, and either one of the harvester ant species compared with the honey ant species was significantly aggregated. The aggregation of these species could be the result of mutualistic interactions, but mutualism is inconsistent with the trends in the levels of aggregation. It seems more likely that these species are interspecifically aggregated because they are avoiding conspecifics more relative to other species based on the diet overlap between them.

An alternate mechanism that could produce the observed spatial patterns is competition for nest space. It may be that physical dimensions of the ant's underground nests determine the minimum distance between colonies. Different species could be packed together closely, if their nests were structured differently. For example, one species may have shallow nests that resemble disks, while another species may have deep nests that are perhaps conic in shape. Similarly, colonies of the same species would have to be spaced further apart. To fully test this hypothesis, extensive nest excavations would have to be performed. Based on the limited information available on the nest size of *V. pergandei*, this argument cannot be refuted, since one estimate of the diameter of the nest is 15 m, which is roughly equal to nearest-neighbor distances (Wheeler and Wheeler 1973).The nest packing hypothesis might also explain the diet overlap data if the species with the most similar nest structure were more closely related and had similar diets simply as a secondary consequence. This hypothesis can be tested with colony removal experiments (see below).

Ryti and Case (1984) found further evidence of intraspecific competition in *V. pergandei.* They found that the sum of the colony sizes of nearest neighbors was significantly positively correlated with the nearest neighbor distance. This may indicate that colonies are more productive when they are further from a conspecific (and potential competitor). Better evidence for resource competition is that *V. pergandei* colonies avoided foraging in the same area when resources were scarce but not when resources were abundant. This presumably is a mechanism to reduce interference between neighbors.

More conclusive evidence of competition as a driving force determining colony spacing requires colony removal experiments, which are now in progress. We are using a focal colony technique, in which conspecific neighbors or other species neighbors are removed around a "focal" colony. The removed neighbors are not destroyed, but only kept from foraging by spraying the foragers with insecticide. This methodology lets us specifically test the nest packing hypothesis, since it leaves the underground structure of the nest mostly intact. If the colony sizes of the focal colonies increase relative to controls, then the excluded species must have been suppressing the amount of food available to the other species. The relative effects of such species removals should also be consistent with the diet overlap data. In other words, removing the colonies of *V. pergandei* should have a greater effect on *P. californicus* colonies than would the removal of *M. flaviceps* colonies.

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