Density- and size-dependent spacing of ant nests: evidence for intraspecific competition

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Summary. We present three lines of evidence which each suggest that intraspecific competition has significantly influenced the spacing patterns of *Formica altipetens* colonies. First, nearest-neighbor analysis of nest spacing patterns detected significant uniformity in six of eight plots. Second, there was a significant increase in the distance separating nearest neighbors as ant nest diameters increased. Third, ant nest density predicted substantial variation in the colony dispersion index, indicating the existence of a dispersion continuum at our study site.

Key words: *Formica altipetens* – Intraspecific competition – Nearest-neighbor analysis – Nest size and density

Spatial arrangements of plant and animal populations provide insight into the intra- and interspecific interactions operating within communities (MacArthur 1972; Whittaker 1975; Holldobler 1976; Holldobler and Lumsden 1980; Brown 1981; Levings and Traniello 1981). Here, we consider the spatial patterns of ant colonies. A major factor contributing to the fitness of ant colonies is nest location, as site quality determines both the reproductive and foraging environment (Wheeler 1910; Carroll and Janzen 1973; Bernstein and Gobbel 1979; Brian 1983). Favorable foraging areas depend not only on the distribution of food but also on the presence of neighboring conspecific colonies. Uniform spacing of nests can reduce overlap of foraging areas, thereby minimizing intraspecific competition when colony density is high (Bernstein and Gobbel 1979; De Vita 1979; Harrison and Gentry 1981; Levings and Franks 1982; Ryti and Case 1984, 1986; Sudd and Franks 1987).

While numerous studies have documented ant nest dispersion patterns (see review by Levings and Traniello 1981; Harrison and Gentry 1981; Ryti and Case 1984, 1986), few have considered the impact of colony size and density on spacing patterns (but see Waloff and Blackith 1962; Ryti and Case 1986). Assessing the impact of colony size and density allows for more precise evaluation of spatial patterns and factors responsible for generating such patterns.

We studied the dispersion patterns of *Formica altipetens* Wheeler (Hymenoptera: Formicidae) colonies in northern Arizona. The goals of our study were to determine 1) the dispersion pattern(s) of *F. altipetens*, 2) the effect of the

size of neighboring ant nests on the distances separating them, and 3) the impact of ant nest density on the type and strength of dispersion pattern.

Methods

We mapped ant nests at the base of Fern Mountain in Hart Prairie (2700 m elevation), approximately 40 km north of Flagstaff, Coconino County, Arizona. Throughout the study area, *F. altipetens* was the only ground nesting ant species present. This species does not have multiple nest entrances (R.R. Snelling, unpublished work), through it does occasionally construct small satellite nests which are easily distinguished from the main entrance (unpublished work, see below). We established eight 20 × 20 m plots for dispersion analysis; seven were in open prairie habitat and one was completely within the outer portion of an aspen clone (*Populus tremuloides*). We searched each plot and the surrounding area for a minimum of one man-hour and flagged all nests. As a rough estimate of ant colony size, we recorded the diameter of the actively maintained portion of all nests within the plots. We believe this estimate is resonable, given that we are 1) working with a single species at one elevation and 2) using the estimate as a relative rather than absolute measure. We considered only major nest entrances as separate nests; small satellite nests at the bases of aphid-infested *Potentilla hippiana* were not counted [see Wheeler (1910) for a discussion of "aphid tents"].

After nests within the plots were located and marked, we measured the distance from each nest to its nearest neighbor. Sinclair (1985) has noted that significant edge effects can result when conducting nearest-neighbor analysis. That is, the nearest-neighbor distance for nests near a plot boundary will be artificially large if the neighbor must be within the plot. To correct for this edge effect, we used the true nearest neighbor, whether it was located inside or outside the plot.

We evaluated the dispersion pattern of *F. altipetens* in study plots using Clark and Evans' (1954) nearest-neighbor measure, R, which can range from 0 (perfect aggregation) to 2.1491 (perfect hexagonal uniformity); a value of 1.0 indicates random dispersion. The statistical significance of R is tested using the z transformation.

To assess the impact of plot vegetation on nest dispersion patterns, we collected vegetation data from all adjacent plots that exhibited different nest dispersion patterns. This was accomplished by sampling plot vegetation at 1 m inter-

Table 1. Nearest-neighbor analysis summary. Significant dispersion index (R) values greater than 1.0 indicate overdispersion; non-significant values indicate random dispersion

Plot #	Nest density (nests/m²)	Mean nearest-neighbor distance (meters) ±1 standard error	R-Value
1	0.053	3.36±0.23	1.540 ***
2	0.048	2.75±0.17	1.199 ns
3	0.058	2.63±0.24	1.260 *
4	0.073	2.75±0.16	1.479 ***
5	0.033	3.08±0.36	1.112 ns
6	0.045	3.18±0.21	1.347 **
7	0.070	2.93±0.20	1.550 ***
8	0.085	2.44±0.13	1.420 ***

$* P<0.03$; $** P<0.005$; $*** P<0.0005$

vals along two diagonal transects. At each interval, we noted the plant species present at three points (on the transect line and one meter to either side of the line). Thus, for each sampled plot we determined the plant species present at 174 points. We then calculated the proportion of each plot covered by dominant plant species to determine if major vegetational differences existed between adjacent plots having different dispersion patterns. In order to evaluate one-tailed hypotheses we performed binomial tests for comparisons of two proportions as described by Zar (1984:395).

We analyzed the relationship between the combined size of 87 neighboring ant nest pairs and the distance separating them. This was accomplished by generating a linear regression of combined nest diameter against nearest-neighbor distance.

We generated a linear regression of ant nest density on the eight plots against Clark and Evans' (1954) dispersion index value to evaluate the relationship between colony density and spatial arrangement.

Results and discussion

Ant nest spacing patterns

Results from nearest-neighbor analysis provide the first line of evidence suggesting that intraspecific competition is or has been sufficiently strong to generate and maintain uniformly dispersed *F. altipetens* colonies at Hart Prairie. In six of eight plots (1, 3, 4, 6, 7, and 8) we detected significant uniformity in the spacing of ant nests (Table 1). The advantage of such uniformity may be that overlap of foraging areas, and therefore the potential for competition, is reduced (Bernstein 1975; Bernstein and Gobbel 1979; De Vita 1979; Harrison and Gentry 1981; Levings and Franks 1982).

A number of potential competitive mechanisms have been described that generate and maintain uniform spacing of ant nests. First, workers from neighboring colonies may kill or eject founding queens (Holldobler 1976; Brian 1983). Second, workers from neighboring nests may act aggressively toward recently established and/or already existing colonies (Wilson 1971; Mabelis 1979). Third, neighboring colonies may deplete surrounding resources such that recently established nests fail to acquire sufficient resources for themselves.

The failure of nests on two plots (2 and 5) to exhibit uniform spacing was correlated with unique characteristics of plant distribution in those plots. Clonal mats of *Potentilla hippiana* covered a large portion of plot 2 and a binomial comparison of proportions indicated that this proportion was significantly greater than that found in closely adjacent plot 7, which had overdispersed nests ($z=6.4$, $P<0.0002$). Areas in the plot that were densely covered with these mats lacked ant nests, suggesting that either the *Potentilla* mats are difficult for *F. altipetens* to colonize or the areas offer an insufficient amount or quality of food for colonies to sustain themselves. If this were true, it would reduce the useable area within the plot and bias the nearest-neighbor test away from uniformity. When these monospecific *Potentilla* mats were excluded from the plot, the available area of plot 2 became 375 m² rather than 400 m². The recalculated R value for this reduced area was 1.245 (instead of 1.199) and indicates significant uniformity in the spacing of nests ($P<0.05$). Waloff and Blackith (1962) discuss a similar impact of the grass *Arrhenatherum* sp. on density and dispersion of *Lasius flavus* nests.

Random nest dispersion in plot 5 was correlated with an abundance of aspen in the plot. Unlike the other seven plots, plot 5 was located completely within the outer portion of an aspen clone. Vegetation transect data indicated that there was a significantly greater proportion of aspens on plot 5 than in closely adjacent plot 6, which had uniformly dispersed nests ($z=4.05$, $P<0.0002$). Plot 5 was also unique in that it contained only 13 large nests whereas the other plots contained from 17 to 34 nests that ranged widely in size. Given that *F. altipetens* nest abundance within the aspen clone decreased toward the center, we suspect that plot 5 was located in the open prairie when it was initially colonized by *F. altipetens* and was subsequently invaded by the expanding aspen clone. Further colonization by this ectothermic insect probably did not occur after invasion by the aspen clone due to the presence an inadequate thermal regime.

The validity of this hypothesis is in part dependent on the life span of ant colonies and the age of aspen ramets within plot 5. While the longevity of *F. altipetens* colonies is unknown, the large size of their ground nests suggest that they persist many years. In addition, Wilson (1971) reports that some *Formica* colonies can persist for 20–65 years. Tree ring analysis indicated that most aspen ramets within plot 5 were from 10–20 years old (G.D. Martinsen, unpublished work). Thus, the large ant nests in plot 5 may well have become established before the aspen clone expanded into the area.

Ant nest size and nearest-neighbor distances

The second line of evidence which suggests the occurrence of intraspecific competition is our finding that the distance separating neighboring ant colonies is a function of their combined diameters (Fig. 1). These results more directly describe the uniform dispersion patterns exhibited by *F. altipetens*. Because larger ant colonies require greater food resources (Wilson 1971; Mabelis 1979), they should be separated by greater distances, assuming that surrounding resources are limited. For example, Mabelis (1979) found that larger *Formica polyctena* colonies have larger territories and are more aggressive towards intraspecific neighbors.
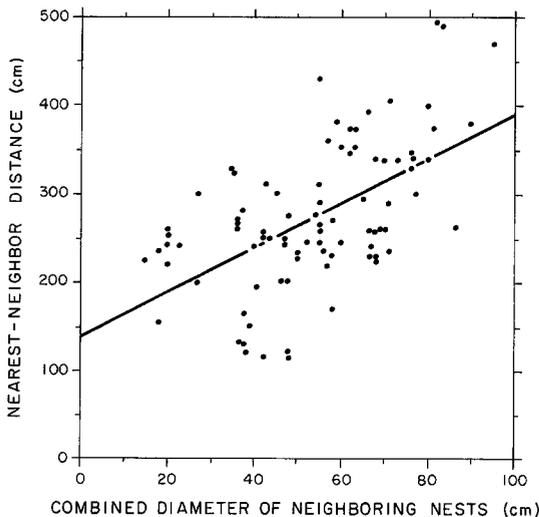
Fig. 1. Nearest-neighbor distances plotted as a function of the combined diameter of neighboring nest pairs ($y=140.0+2.49x$; $r=0.565$; $P<0.0005$)

Fig. 2. Colony dispersion index values plotted as a function of ant nest density per plot ($y=0.996+6.33x$; $r=0.663$; $P<0.05$). The open circle is from Bernstein and Gobbel (1979) but was not used to calculate the regression line

Two other studies also have considered the relationship between the size of neighboring ant colonies and the distance separating them. For *Lasius flavus*, Waloff and Blackith (1962) were unable to detect an association between the size of nests and the distance to their nearest neighbor. However, the authors neglected to consider the size of neighboring nests in this analysis. In the second study, Ryti and Case (1986) found that *Veromessor pergandei* and *Pogonomyrmex californicus* both exhibit a positive association between the combined size of neighboring intraspecific colonies and the distance separating them.

Others factors undoubtedly contribute to the distance separating neighboring ant nests. This is illustrated by Fig. 1, which shows that 70% of the variation in the distance separating neighboring nests is not explained by combined nest diameters. Our crude estimates of ant colony size is a probable explanation for much of this unexplained variation. Another potential explanation is that the abundance of ant resources in our study plots may have been locally variable and that this resulted in variability in nearest neighbor distances.

Density of ant nests and dispersion index values

The third line of evidence which suggests the occurrence of intraspecific competition is that the degree of nest uniformity, as measured by nearest-neighbor analysis, increased with nest density (Fig. 2). Thus, we have shown the existence of a dispersion continuum in our study area. This pattern suggests that as intraspecific density increases, resources become more limiting, the intensity of competition increases, and increased uniformity in the spacing of colonies is favored because it minimizes these negative interactions.

The findings of Waloff and Blackith (1962) suggest that similar spatial relationships may hold for other ant species as well. They found that the dispersion of *Lasius flavus* nests was random at a low density site and uniform at a high density site.

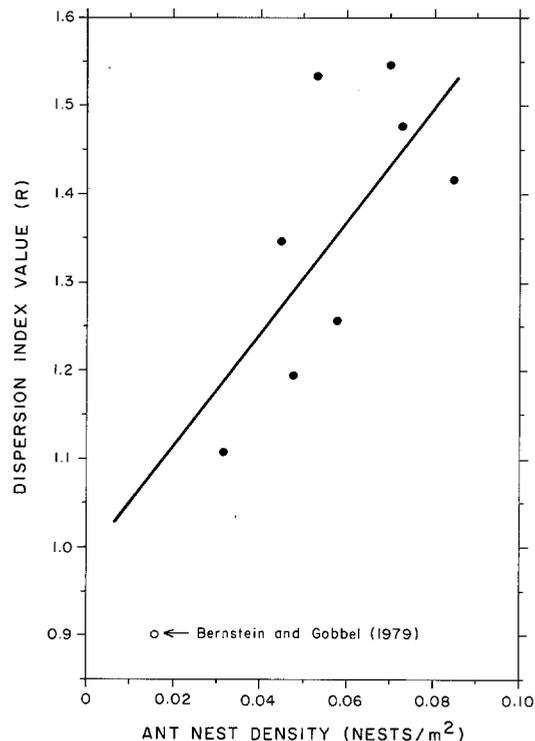Bernstein and Gobbel (1979) studied the dispersion of *F. altipetens* nests in the Great Basin Desert, where they

occurred at lower density (0.0157 nests per m^2) than on any of our plots at Hart Prairie. The dispersion index for their plot was also extremely low (R=0.9). This dispersion-density relationship nicely fits into our regression analysis presented in Fig. 2 and inclusion of their data actually increases the R^2 value from 44% to 67%. Thus, *F. altipetens* may also exhibit a dispersion continuum throughout its entire range, with high nest density and overdispersion at high elevations, and low density and random dispersion at low elevation.

References

Bernstein RA, Gobbel M (1979) Partitioning of space in communities of ants. J Anim Ecology 48:931–942

Brian MV (1983) Social Insects; Ecology and Behavioral Biology. Chapman and Hall, London

Brown JH (1981) Two decades of homage to Santa Rosalia: toward a general theory of diversity. Amer Zool 21:877–888

Carroll CR, Janzen DH (1973) Ecology of foraging ants. Ann Rev Ecol Syst 4:231–257

Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453

De Vita J (1979) Mechanisms of interference and foraging among

colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave desert. Ecology 60:129–737

Harrison JS, Gentry JB (1981) Foraging patterns, colony distribution, and foraging range of the Florida harvester ant, *Pogonomyrmex badius*. Ecology 62:1467–1473

Holldobler B (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav Ecol Sociobiol 4:163–181

Holldobler B, Lumsden CJ (1980) Territorial strategies in ants. Science 210:732–739

Levings SC, Traniello JFA (1981) Territoriality, nest dispersion, and ant community structure. Psyche 88:265–319

Levings SC, Franks NR (1982) Patterns of nest dispersion in a tropical ground ant community. Ecology 63:338–344

Mabelis AA (1979) The relationship between aggression and predation in the red wood ant (*Formica polyctena* Forst). Netherlands J Zool 29:451–620

MacArthur RH (1972) Geographical Ecology. Harper and Row, New York

Ryti RT, Case TJ (1984) Spatial arrangement and diet overlap between colonies of desert ants. Oecologia (Berlin) 62:401–404

Ryti RT, Case TJ (1986) Overdispersion of ant colonies: a test of hypotheses. Oecologia (Berlin) 69:446–453

Sinclair D (1985) On tests of spatial randomness using mean nearest neighbor distance. Ecology 66:1084–1085

Sudd JH, Franks NR (1987) The Behavioral Ecology of Ants. Blackie and Sons, Glasgow

Waloff N, Blackith RE (1962) The growth and distribution of the mounds of *Lasius flavus* (Fabricius) (Hymenoptera:Formicidae) in Silkwood Park, Berkshire. J Anim Ecol 31:421–437

Wheeler WM (1910) Ants, their structure, development, and behavior. Columbia University Press, New York

Whittaker RH (1975) Communities and Ecosystems. Macmillan, New York

Wilson EO (1971) The Insect Societies. Harvard University Press, Cambridge

Zar JH (1984) Biostatistical Analysis. Prentice-Hall, Englewood Cliffs