ORIGINAL PAPER

Eldridge S. Adams · Walter R. Tschinkel

Spatial dynamics of colony interactions in young populations of the fire ant *Solenopsis invicta*

Abstract Newly founded colonies of the fire ant *Solenopsis invicta* compete intensely by brood raids, which result in a rapid reduction of colony density. Experimental plantings of colonies and analyses of sequential maps were used to examine the importance of spatial pattern in the dynamics of young populations. Colony positions were initially clumped in naturally founded cohorts, but were regular in most mature populations. Incipient colonies planted in clumped patterns were more likely to engage in brood raids than colonies planted in regular hexagonal patterns at the same average density. However, contrary to what would be expected if local crowding increased mortality, no significant increases in spatial regularity were observed during brood raiding either in the experimentally planted populations or in a natural population of more than 1200 incipient colonies. These results show that it may be difficult to infer the degree of past or current competition by passive analysis of spatial data even when field experiments show that the probability of mortality depends on local spacing.

Key words Ants · Spatial pattern · Population dynamics · Competition · *Solenopsis*

Introduction

The analysis of the spatial positions of organisms is of interest to ecologists primarily for two reasons. First, the pattern may reflect the past history of interactions and may be used to infer the existence or nature of competition among neighbors (e.g., Waloff and Blackith 1962; Ryti and Case 1986; Kenkel 1988). Second, the spatial pattern of organisms may affect the future course of ecological interactions. If this effect is strong, it may be necessary to include pattern as well as density within models of population dynamics (e.g., Yodzis 1978; Bonan 1988; Pacala 1989).

Nest sites in ant populations are commonly distributed in regular patterns (reviewed by Levings and Traniello 1981), which are often taken as evidence of competition. However, competition among colonies can also produce clumped spatial patterns, or patterns that are apparently random, even in homogenous habitats (Pielou 1960; Lepš and Kindlmann 1987; Ryti and Case 1992). Thus, the degree of spatial regularity cannot be used as a measure of the intensity of competition and failure to observe regular patterns cannot be taken as evidence that competition is weak or absent. Various other methods have been suggested which may have greater power to detect the effects of competition than simple nearest neighbor analyses. These include testing for correlations between colony size and spacing (Waloff and Blackith 1962; Ryti and Case 1986; Cushman et al. 1988; see Pielou 1960 for a similar test with plants) or between density and spacing (Cushman et al. 1988; Ryti 1991).

An alternative approach is to test for the changes in spatial pattern that are expected to accompany density-dependent mortality. In populations of sessile organisms, neighborhood competition can increase the degree of spatial regularity since mortality falls most heavily on individuals that are especially close to their neighbors. Simulation models of competition among sessile organisms show that even-aged cohorts become increasingly regular with time (Slatkin and Anderson 1984; Lepš and Kindlmann 1987). By contrast, when mortality is spatially random, random patterns of spatial arrangement result whether the original pattern is clumped, random, or regular (Lepš and Kindlmann 1987). Thus, the change in spatial pattern may provide

E. S. Adams (✉)
Department of Biology, University of Rochester, Rochester, NY 14627, USA

W. R. Tschinkel
Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA

better evidence for competition than a "snapshot" analysis at any particular point in time (Ford 1975; Kenkel 1988). In ants, the degree of spatial regularity is sometimes higher in mature populations than in young ones (Bartz and Hölldobler 1982; Ryti and Case 1988; Rissing and Pollock 1991). While the mechanisms of spatial dynamics in these cases are not fully understood, shorter distances to nearest neighbors can be associated with increased likelihood of competitive struggles (Hölldobler 1981), colony mortality (Thurber et al. 1993), or migration (De Vita 1979). However, Ryti and Case (1988) found no significant increase in regularity associated with mortality of colonies in the ants *Veromessor pergandei* or *Mymecocystus flavipes* between colony initiation and the first signs of worker activity.

This study examined the dynamics of spatial pattern in young populations of the fire ant *Solenopsis invicta* during "brood raids," a form of competition among incipient colonies (described below). Two approaches were adopted. First, we tested whether the regularity of spatial pattern increased significantly during brood raid competition. Second, a replicated field experiment tested whether the spatial pattern of colonies affects the frequency of brood raids and colony survivorship. To our knowledge, spatial pattern has not previously been experimentally manipulated in social insect populations to measure its effects upon population processes, although this method has been used in a few cases with other taxa (Weiner 1985; Blower and Roughgarden 1989). Finally, we comment on the power of these and other spatial analyses to detect competition within ant populations.

Materials and methods

Study organism

Colonies of the single-queen, or "monogyne", form (Ross and Fletcher 1985a) of *S. invicta* are founded by newly mated queens shortly after nuptial flights. Queens fly to areas of suitable habitat, drop their wings, then excavate chambers in the soil within which they lay eggs and rear the first cohort of workers (Markin et al. 1972). In areas where *S. invicta* is common, queens may establish dense cohorts of incipient colonies in recently disturbed habitats (Tschinkel 1992a). When the first workers emerge, colonies compete intensely by "brood raids", in which workers remove brood from nearby colonies to be reared within the raiding colony (Tschinkel 1992a, b). In most brood raids, the raided colony loses nearly all of its brood and its workers join the winning colony. Abandoned queens then emigrate or die (Tschinkel 1992a; Adams and Tschinkel 1995). Using data from a naturally occurring field population, Tschinkel (1992a) estimated that most colonies engaged in at least one brood raid and that brood raiding was the primary source of mortality during the first few weeks of life. Brood raids have also been documented in other ant species (Hölldobler 1981; Bartz and Hölldobler 1982; Rissing and Pollock 1987, 1991).

Within a few weeks or months, brood raiding ceases and surviving colonies begin to compete instead by defending discrete foraging territories (Adams and Tschinkel 1995). Mature colonies

defend territories intraspecifically (Wilson et al. 1971), within which they scavenge or prey upon arthropods and collect seeds and other plant material (Tenant and Porter 1991).

In a second social form of *S. invicta*, known as the multiple-queen or "polygyne" form, colonies appear to reproduce by budding, rather than through independent colony founding by recently mated queens (Ross and Fletcher 1985a; Vargo and Porter 1989). The development of spatial pattern will therefore follow different rules. At our study sites near Tallahassee, Florida, and elsewhere in Leon county, only the monogyne form is found (Porter 1992; E. Adams and W. Tschinkel, personal observations).

Study sites

A large population of incipient colonies was mapped in a 30 × 30 m plot on a construction site in Tallahassee, Florida. These nests were founded naturally by mated queens in an area with few mature colonies. Due to the sparse vegetation, it was possible to detect active nests by watching ant activity and by searching for the small piles of excavated soil characteristic of newly excavated nests. Details are described by Tschinkel (1992a).

Mature colonies were mapped in open pasture approximately 1 km outside the Tallahassee city limits. No pesticides have been applied at this site since the arrival of *S. invicta* to the area in the late 1950s. Nine circular plots were established, each 72 m in diameter. Within each plot, all active fire ant colonies were mapped from the center using a compass and tape measure. Because *S. invicta* colonies excavate mounds of soil at their nest sites, all but the smallest colonies – those less than 1 year old – can be located with ease. Occupation of each mound by *S. invicta* was confirmed by poking a wire stake into the mound, a disturbance which causes workers to rush out of the nest.

Tests for non-random spatial patterns

Analyses of spatial pattern were based on the distances from each colony to the nearest neighboring colony. The distributions of nearest neighbor distances expected under random placement were generated by computer simulation. For a given map of colony positions, points equal in number to the observed number of colonies were cast randomly into an area corresponding in size and shape to the census areas. The distance from each point to its nearest neighbor was then calculated. This process was repeated for 500 replicate simulations to calculate the expected value and the 95% confidence interval for the mean nearest neighbor distance. If the observed mean nearest neighbor distance fell outside of this interval, it was concluded that the spatial pattern was non-random. To illustrate spatial patterns in greater detail, the complete distribution of nearest neighbor distances was plotted for a single cohort of incipient colonies and for a single study plot within the mature population (Fig. 1). This figure also shows the expected distribution of nearest neighbor distances for randomly placed colonies generated by 500 Monte Carlo simulations.

The Clark and Evans (1954) statistic was used to summarize spatial patterns. This statistic is the ratio of the observed mean nearest neighbor distance to the mean nearest neighbor distance expected for a randomly distributed population. Values significantly below 1 indicate clumping; values significantly above 1 indicate regularity.

For all Monte Carlo simulations, an improved pseudo-random number generator was used. The routine is described by Press et al. (1989) under the name "Ran1".

Tests for spatially non-random mortality

To test whether competition among colonies increased the degree of spatial regularity, the null hypothesis of spatially random mortality was simulated. This test used sequential maps of colony positions where the later maps included the survivors of those
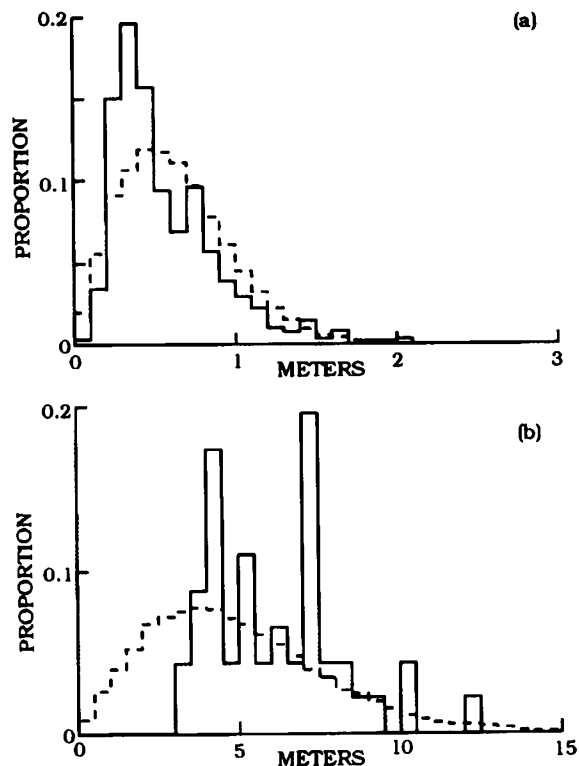
Fig. 1a, b Frequency histograms of observed nearest neighbor distances (*solid lines*) and those expected for random colony placement (*dotted lines*). **a** A cohort of 592 incipient colonies in a 30 m × 30 m plot showed significant clumping. **b** The positions of 46 mature colonies in a circular plot with a 72 m diameter were significantly regular

colonies present on the original map. Computer simulation was used to test whether the spatial pattern, as quantified by the mean nearest neighbor distance, differed significantly from the pattern expected if mortality were spatially random (Kenkel 1988).

Each simulation began with the observed map of initial colony positions within a rectangular region. Colonies were selected randomly and removed until the number of survivors remaining matched the observed number in the field population. The process was repeated for 1000 replicates to generate the expected mean nearest neighbor distances and the upper and lower 95% confidence intervals. The mean nearest neighbor distance was then calculated for the observed map with the same final number of survivors. If the observed values fell outside the 95% confidence interval, this was taken as evidence that mortality was spatially non-random.

To examine the power of this statistical procedure, neighborhood competition was simulated following the algorithm of Slatkin and Anderson (1984). Beginning with an initial map of colony positions, the smallest nearest neighbor distance was found. One of the two colonies separated by this distance was chosen randomly and removed. This process was repeated until the observed number of survivors remained.

During the period of brood raiding, several cohorts of new colonies were established during successive nuptial flights (Tschinkel 1992a). The change in spatial pattern was analyzed for each cohort separately. However, survivors of early cohorts sometimes interacted with colonies from later cohorts, which may have affected their combined spatial distribution. Therefore, in a second series of analyses, maps were constructed which included all colonies active at a particular census date, regardless of colony age. Changes in the spatial patterns of these assemblages were then compared to those expected for spatially random mortality, as described above.

Collection and rearing of queens

Mated queens were collected following nuptial flights in Tallahassee, Florida. Queens that have mated and dropped their wings can be collected in large numbers from parking lots, where they are unable to dig beneath the soil. Queens were collected within a few hours following flights, separated, and kept individually without food in moist plaster nests or in test tubes provided with moist cotton. In these conditions, queens lay eggs and rear their first cohort of workers using stored energy reserves (Tschinkel 1993). When the first workers eclosed, colonies were selected for planting. To reduce size variation among planted colonies, colonies in which the queen died, produced diploid males (Ross and Fletcher 1985b), or produced fewer than ten pupae or workers were rejected. Colonies were randomly assigned to treatment. Each colony was transferred to a small plaster block, measuring approximately 5 × 2 × 2 cm, with a 2-mm hole drilled through the long axis. A chamber 12 mm in diameter and 15 mm deep was drilled in one end. Each nest was wrapped temporarily in paper to prevent escape by the workers or queens during transport to the field.

Preparation of field sites

Colonies were planted in an open spray-irrigated field at the Mission Road Biological Station of Florida State University. Prior to planting, the site was tilled, flattened, and raked to reduce vegetation cover and to homogenize conditions across replicate plots. The pesticide Amdro (American Cyanamid, Princeton, N.J.) was broadcast over the experimental area and at least 20 m beyond in each direction more than 60 days before the experimental plantings. Amdro degrades rapidly in sunlight or water, leaving no detectable toxic residue after several days (Apperson et al. 1984). Transects of food baits confirmed that this treatment was effective in removing fire ant colonies.

Colonies were planted in replicate plots in one of two spatial arrangements. Each plot included 52 colonies. In the "regular" treatment (Fig. 2a), colonies were planted in a hexagonal pattern with 50 cm between nearest neighbors. The pattern for the "clumped" treatment (Fig. 2b) was a Cox process (Diggle 1983), generated as follows. Ten points were randomly chosen within a square. The 52 colonies were randomly assigned to these points. The colonies assigned to a point were distributed around it in a bivariate normal distribution with a mean and standard deviation of 15 cm. The scale of this clumped arrangement was then adjusted until the area of the least convex polygon enclosing the 52 positions was identical to the area of the least convex polygon enclosing the 52 positions in the regular treatment (8.88 m^2). Thus, the average density of colonies was the same for both treatments. This method for generating a clumped pattern was chosen because it produced a pattern contrasting strongly with the regular pattern and roughly consistent with natural patterns of incipient colony clumps.

Six replicate plots were established for each of the two spatial patterns. Adjacent plots were separated by at least 5 m; no raids were seen between plots. To allow rapid searches of colony entrances, a 12 cm wooden marker and a 4 × 4 cm metal tag were used to mark each nest site. Plots were randomly assigned to treatment. Regular and clumped assemblages were planted in pairs on the same day. A hole was excavated to a depth of 7 cm at each site selected for colony planting. The plaster block containing the colony was unwrapped and inserted into the hole so that the large chamber was at the bottom, mimicking the brood chamber normally excavated by the queens. The artificial nest was then covered with soil. To maintain surface soil moisture, the site was watered on any day that it did not rain. All but one of the 624 colonies survived planting. Workers began to emerge, forage, and raid within 24 h following planting.

Tschinkel (1992a) found that most raids occur in the morning and evening and continue for more than 30 min. On each day of the experiment, all colonies on all plots were surveyed at least once per hour during the morning (8:00 a.m.–1:00 p.m.) and
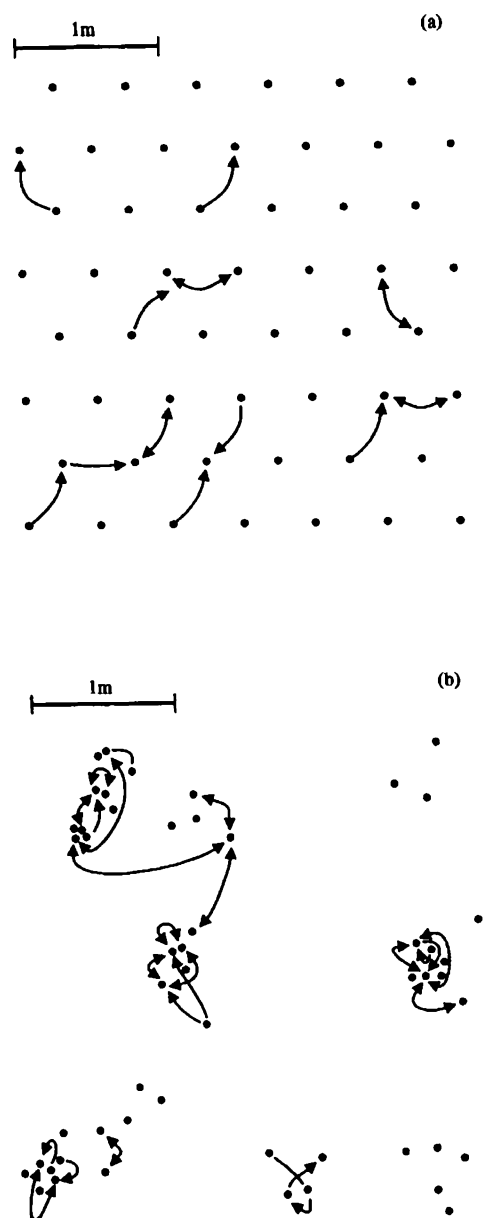
Fig. 2 Brood raids among **a** regularly spaced colonies and **b** clumped colonies. Each *circle* represents the position of a planted colony. *Lines* connect colonies between which workers moved and *arrows* indicate the directions in which broods were carried. The examples shown are the replicates with the greatest numbers of raids

evening (6:30–7:30 p.m.), except during heavy rains. Colonies were scored as active or inactive and, when brood raids were seen, maps were drawn of the patterns of movements of workers and brood.

Colonies were judged to be active if an entrance hole was visible above the buried artificial nest. Previous work showed that entrance holes can persist past the death of the colony. Therefore, at the end of each day, entrance holes were sealed with moist soil. Whereas the entrances of dead colonies remained sealed, active colonies quickly excavated through these plugs, allowing confirmation of worker activity. When brood raids were seen, additional surveys were added to allow more detailed description of raiding paths. To avoid bias, all plots were inspected during each additional survey.

The frequency of raids peaked 2–3 days after planting, then declined rapidly. Regular monitoring was continued for 3 days after the last raid was seen.

Results

Spatial patterns of colonies in young and old populations

All naturally founded cohorts of incipient colonies were significantly clumped (Table 1). For the largest cohort, the mean nearest neighbor distance (56 cm) was less than expected for random placement (63 cm), with an excess of colonies within 50 cm of their nearest neighbor (Fig. 1a). Slightly fewer colonies than expected were found within 20 cm of their nearest neighbor. By contrast, colony positions in eight of the nine mature population sites were significantly regular (Table 1). The distribution of nearest neighbor distances for a representative example is shown in Fig. 1b. The mean nearest neighbor distance (6.14 m) was greater than expected from random placement (4.98 m), with a shortage of colonies within 3.5 m of their nearest neighbors.

Dynamics of spatial patterns during brood raids

Patterns of change in spatial pattern during the period of brood raiding were consistent with spatially random mortality. A map of the largest cohort is shown in Fig. 3 and the changes in spatial pattern for this cohort are shown in Fig. 4. Colonies in this cohort were initially

Table 1 Mean nearest neighbor distances (*NND*) for four cohorts of incipient colonies in a 30 × 30 m plot, and mature colonies in nine circular plots (each being 72 m in diameter). For each data set, the expected mean NND and the *P* value were derived from 500 Monte Carlo simulations of random placement. A Clark and Evans index significantly less than 1.0 indicates clumping; values significantly greater than 1.0 indicate regular spacing

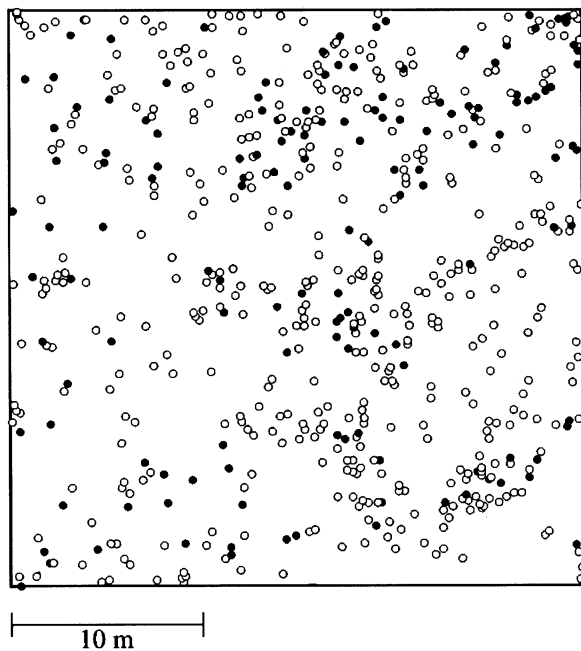| Number of colonies	Observed mean NND (m)	Expected mean NND (m)	Clark and Evans index
Incipient colonies			
592	0.56	0.63	0.89**
285	0.81	0.91	0.89**
300	0.82	0.89	0.92**
55	1.61	2.13	0.76**
Mature colonies			
46	6.14	4.98	1.23*
47	5.63	4.91	1.15
32	7.39	6.04	1.22*
47	6.07	4.91	1.24**
38	6.58	5.51	1.19*
40	6.99	5.34	1.31**
42	6.28	5.22	1.20*
39	6.89	5.41	1.27**
41	6.49	5.28	1.23**

*$P < 0.05$; **$P < 0.01$

Fig. 3 Positions of a single cohort of naturally occurring incipient colonies within a 30×30 m plot. *Filled circles* represent colonies that survived at least 25 days after emergence of the first workers; *open circles* represent colonies that died within 25 days. Survivors were a spatially random subset of the original cohort
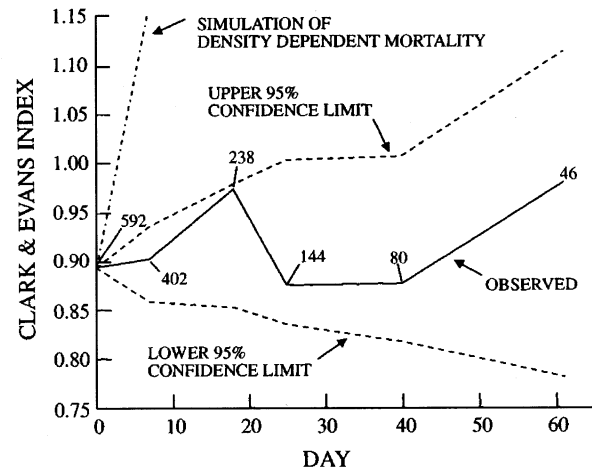

Fig. 4 The spatial pattern of a cohort of naturally occurring incipient colonies changed little as colonies died. The observed Clark and Evans index (*solid line*) remained within the 95% confidence intervals for random mortality (*dashed lines*). The number of surviving colonies is shown for each date. When density-dependent mortality was simulated, the Clark and Evans index passed well outside the 95% confidence envelope after reduction to 402 survivors and continued to rise thereafter (see text)

clumped. During the first 61 days, 92% of the colonies died, but the Clark and Evans index increased only slightly to 0.98, close to the value expected for random placement. The mean nearest neighbor distance at each census date stayed within the 95% confidence intervals generated by simulations of random mortality.

Similar results were obtained for the other cohorts (Table 2). No evidence was found for non-random changes in spatial pattern for any cohort or for any combination of cohorts active at the same dates (Table 3). Of the 12 experimentally planted colony assemblages, 11 showed no evidence of non-random changes in pattern. The mean nearest neighbor distances on the 12th plot, which was planted in a clumped

Table 2 Changes in the observed mean nearest neighbor distances (*NND*) for four naturally founded cohorts of incipient colonies compared to those expected from spatially random mortality. Each cohort was composed of colonies founded during a single nuptial flight; cohort designation is the same as in Tschinkel (1992a). The original positions were mapped at the first signs of worker activity. The observed mean NND at each subsequent census was compared to the expected mean NND and 95% confidence intervals generated by 1000 simulations of spatially random mortality for each cohort (see text). In no case did the observed mean NND differ significantly from the expectation for random mortality

Number of colonies	Date	Mean NND (m)		
		Observed	Expected from random mortality	95% confidence limits
Cohort A: colonies founded May 5; first mapped June 20				
592	Original positions	0.56		
402	June 27	0.69	0.69	0.66–0.72
238	July 8	0.97	0.91	0.85–0.98
144	July 15	1.13	1.20	1.08–1.32
80	July 30	1.53	1.65	1.43–1.87
46	August 20	2.30	2.25	1.83–2.63
Cohort B: colonies founded June 4; first mapped June 28–July 7				
285	Original positions	0.81		
188	July 8	1.00	1.00	0.94–1.08
134	July 15	1.23	1.21	1.10–1.34
63	July 30	1.86	1.85	1.55–2.14
30	August 20	2.70	2.82	2.17–3.53
Cohort C: colonies founded June 13; first mapped June 29–July 13				
300	Original positions	0.82		
230	July 15	0.93	0.92	0.87–0.97
108	July 30	1.49	1.39	1.22–1.56
56	August 20	2.23	2.00	1.68–2.31
Cohort D: colonies founded approximately July 4; first mapped July 16–July 30				
55	Original positions	1.61		
27	July 30	2.18	2.40	1.67–3.12
13	August 20	4.16	3.67	2.07–5.38

Table 3 Changes in the observed mean nearest neighbor distances (*NND*) for assemblages of incipient colonies compared to those expected for spatially random mortality. Each assemblage includes all colonies active on the first census date, regardless of colony age (date of mating flight). Expected values and 95% confidence intervals were derived from Monte Carlo simulation, as in Table 2. In no case did the observed mean NND significantly differ significantly from the expectation for random mortality

Number of colonies	Date	Mean NND (m)		
		Observed	Expected from random mortality	95% confidence limits
Assemblage A (all colonies alive on June 27)				
403	June 27	0.69		
239	July 8	0.91	0.90	0.84–0.96
144	July 15	1.13	1.18	1.07–1.30
80	July 30	1.53	1.63	1.42–1.86
Assemblage B (all colonies alive on July 8)				
448	July 8	0.68		
290	July 15	0.82	0.85	0.80–0.89
150	July 30	1.20	1.18	1.07–1.29
Assemblage C (all colonies alive on July 15)				
508	July 15	0.65		
251	July 30	0.94	0.91	0.86–0.97

pattern, were greater than the upper 95% confidence limit for spatially random mortality on the 7th and 8th days following planting, but fell to within the 95% confidence intervals thereafter.

Simulation of strong neighborhood competition produced an increase in spatial regularity of colonies easily detected by the methods used in this paper. When colony mortality was simulated by successive elimination of the smallest neighbor distances (see Methods), the Clark and Evans index rose steadily, passing beyond the 95% confidence envelope for random mortality by the time 402 survivors remained (Fig. 4) and rising to 1.59 after reduction to 46 survivors.

Experimental plantings

Colonies planted in clumped patterns were significantly more likely to engage in brood raids than colonies planted at the same average density in regular hexagonal arrays (40.4% ± 5.9% SE versus 18.7% ± 5.3; t-test, $P < 0.05$; $n_1 = n_2 = 6$). The maximum number of colonies raiding in a single day was greater in clumped populations than in regularly spaced populations (11.8 ± 2.1 versus 4.2 ± 1.1; t-test, $P < 0.02$). Figure 2 depicts brood raids on the clumped and hexagonal plots with the greatest number of raids. The last raid was seen 9 days after the colonies were planted. By the 10th day, the proportion of survivors was lower in clumped populations (62.3% ± 9.3%) than in regular populations (77.9% ± 7.0%), but the difference was not significant (t-test, NS).

Combining data for both treatments, 93% of raids ($n = 129$) involving pairs of colonies were conducted over distances of 50 cm or less, with a maximum raid distance of 132 cm. Of raids simultaneously involving more than two colonies ($n = 65$), 66.2% involved colonies with a separation of 50 cm or less, with a maximum separation of 150 cm.

Discussion

Brood raiding in *Solenopsis invicta*, like other forms of competition in ants, occurs within local neighborhoods. Since colonies are sessile, or move infrequently, the likelihood of competition between two colonies is inversely related to the distance between them. In experimentally planted populations, most brood raids occurred between colonies that were within 50 cm of one another and less than 1% of brood raids occurred between colonies that were more than 1 m apart. Because competition is local, the spatial pattern of the population is an important predictor of the intensity of competition. Experimental plantings, in which pattern was manipulated while keeping average density constant, clearly demonstrated the effects of local arrangements of colonies on competitive interactions.

Despite the strength of the experimental results, the increase in spatial regularity expected in competing populations was not detected either in naturally founded cohorts or in experimentally planted nest assemblages. Simulation studies have shown that competition within a cohort of sessile entities can increase the spatial regularity of the population (Slatkin and Anderson 1984; Lepš and Kindlmann 1987). Mortality of crowded individuals should diminish clumping and leave survivors that are comparatively distant from their nearest neighbors. This prediction was not confirmed for cohorts of *S. invicta* competing by the mechanism of brood raiding. No evidence could be found for an increase in the degree of spatial regularity during "self-thinning" of the *S. invicta* population whether cohorts were considered individually or in aggregate. Despite the death of more than 92% of incipient colonies, spatial pattern changed only slightly and the changes were entirely consistent with spatially random mortality. Similarly, in the experimentally planted

assemblages of colonies, there was little evidence of increase in spatial regularity, although clear evidence of competition was obtained.

If the intensity of competition depends upon local spacing, why don't young populations of *S. invicta* become more regular with time? Several lines of evidence, reported in Tschinkel (1992a), show that competition was intense within the naturally occurring population analyzed in this study. Brood raids were commonly observed and the estimated number of raids slightly exceeded the number of incipient colonies, accounting for approximately 60% of colony mortality (Tschinkel 1992a). Several alternative explanations can be suggested. First, the search patterns of worker ants are geometrically imperfect. By chance, workers from incipient colonies may bypass their closest neighbor and raid instead a more distant competitor. Examples can be seen in Fig. 2. Second, not all deaths are due to intra-specific competition. Other sources of mortality may be unrelated to incipient colony crowding and may add a spatially random component to mortality that obscures the effects of brood raids. Third, the statistical methods may lack power, so that the effects of spatial pattern are not easily detected by comparison to simulations of random mortality. This does not appear to be the case. Applying the rules of spatially dependent mortality used within Slatkin and Anderson's (1984) model to our initial maps shows that significant increases in regularity could be detected with ease. This model represents an extreme case in which the likelihood of mortality is strongly dependent upon nearest-neighbor distances, but the rapid divergence of this simulation from the confidence envelopes for random mortality (Fig. 4) shows that milder forms of spatially dependent mortality could also be detected.

A further possibility is that spatial regularity may not increase with time if, in natural circumstances, local colony density is correlated with confounding factors that affect mortality rates in a contrary manner. Natural study sites are not homogeneous. When choosing nest-sites, recently mated queens of *S. invicta* respond to particular features of micro-topography, such as small ridges and hills (Tschinkel and Howard 1983). If queens are adept at selecting sites where colony survival is enhanced, there may be a positive association between incipient colony density and site quality. In this case, the effects of crowding on mortality may be offset by advantages of the selected sites. Similarly, queens in more crowded areas often cooperate in colony founding and as a result produce larger worker forces (Tschinkel and Howard 1983). Thus, colonies that are tightly clustered may grow faster than colonies that are comparatively distant from their neighbors. This too may reduce mortality rates of crowded colonies in naturally founded populations. However, in the experimental study, all colonies were established by a single queen and colony positions were determined by the experiment design, rather than by the queens' responses to habitat variation.

Since spatial regularity did not increase during brood raid competition, the regular patterns seen in mature populations of *S. invicta* (Fig. 1b; Table 1) must develop at a later stage, probably due to territorial competition. Several mechanisms are possible. Colony mortality continues after the end of brood raids and there is considerable reduction in density as the population ages. Spatially dependent mortality during this later stage of competition may increase the regularity of colony positions. In addition, as new cohorts of mated queens arrive in subsequent years, successful colony establishment near mature colonies may be inhibited (Hölldobler 1981). Finally, colony relocation, which is frequent in *S. invicta* (Hays et al. 1982), may tend to increase average nearest neighbor distances, as in some other ant species (De Vita 1979).

There is probably no fully reliable method to measure the intensity of competition from spatial data alone. Competition can produce regular patterns, random patterns, or clumped patterns (Pielou 1960; Lepš and Kindlmann 1987; Ryti and Case 1992). Cushman et al. (1988) and Ryti (1991) have suggested that correlations between colony density and spatial regularity can be used to test for competition among colonies. While positive correlations between these variables have been convincingly demonstrated within some ant populations (Cushman et al. 1988; Ryti 1991), the opposite pattern is also possible. Consider a series of study sites which include both young and old populations of *S. invicta*. Recently founded populations have high densities of clumped colonies and older populations have low densities of regularly spaced colonies (e.g., Fig. 1). Thus, there may be a negative correlation across sites between colony density and the degree of spatial regularity, even when mortality is density dependent. The comparison of sequential maps is potentially a more powerful approach, yet in this study, no evidence of competition could be detected by this method.

Many of these problems can be solved if data on colony sizes are collected along with measurements of density and pattern. Nearest neighbor distances are sometimes greater among large colonies than among small ones (e.g., Pontin 1961; Waloff and Blackith 1962; Wood and Lee 1971; Boomsma et al. 1982; Ryti and Case 1986; Cushman et al. 1988). Even among young colonies, brood raids can drive rapid increases in size variation as brood and workers concentrate within a few victorious nests (Tschinkel 1992a; Adams and Tschinkel 1995). This in itself may explain why competition does not drive more conspicuous changes in spatial pattern. Although brood raid competition is more intense within local clumps, the survivors of these raids are enlarged and may subsequently experience lower rates of mortality than colonies that grow in comparative isolation. This suggests that the creation of size variation among competing colonies is a critical aspect of population dynamics in ants.

References

Adams ES, Tschinkel WR (1995) Density-dependent competition in fire ants: effects on colony survivorship and size variation. J Anim Ecol (in press)

Apperson CS, Leidy RB, Powell EE (1984) Effects of Amdro on the red imported fire ant (Hymenoptera : Formicidae) and some nontarget ant species and persistence of Amdro on a pasture habitat in North Carolina. J Econ Entomol 77: 1012–1018

Bartz SH, Hölldobler B (1982) Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera : Formicidae) and the evolution of foundress associations. Behav Ecol Sociobiol 10: 137–147

Blower SM, Roughgarden J (1989) Parasites detect host spatial pattern and density: a field experimental analysis. Oecologia 78: 138–141

Bonan GB (1988) The size structure of theoretical plant populations: spatial patterns and neighborhood effects. Ecology 69: 1721–1730

Boomsma JJ, Lee GA van der, Have TM van der (1982) On the production ecology of *Lasius niger* (Hymenoptera : Formicidae) in successive coastal dune valleys. J Anim Ecol 51: 975–991

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

Cushman JH, Martinsen GD, Mazeroll AI (1988) Density and size-dependent spacing of ant nests: evidence for intraspecific competition. Oecologia 77: 522–525

De Vita J (1979) Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave Desert. Ecology 60: 729–737

Diggle PJ (1983) Statistical analysis of spatial point patterns. Academic Press, London

Ford ED (1975) Competition and stand structure in some even-aged plant monocultures. J Ecol 63: 311–333

Hays SB, Horton PM, Bass JA, Stanley D (1982) Colony movement of imported fire ants. J Ga Entomol Soc 17: 266–274

Hölldobler B (1981) Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). Behav Ecol Sociobiol 9: 301–314

Kenkel NC (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69: 1017–1024

Lepš J, Kindlmann P (1987) Models of the development of spatial pattern of an even-aged plant population over time. Ecol Model 39: 45–57

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

Markin GP, Collins HL, Dillier JH (1972) Colony founding by queens of the red imported fire ant, *Solenopsis invicta*. Ann Entomol Soc Am 65: 1053–1058

Pacala SW (1989) Plant population dynamic theory. In: Roughgarden J, May RM, Levin SA (eds) Perspectives in ecological theory. Princeton University Press, Princeton, pp 54–67

Pielou EC (1960) A single mechanism to account for regular, random and aggregated populations. J Ecol 48: 575–584

Pontin AJ (1961) Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.) J Anim Ecol 30: 47–54

Porter SD (1992) Frequency and distribution of polygyne fire ants (Hymenoptera : Formicidae) in Florida. Fla Entomol 75: 248–257

Press WH, Flannery BP, Teukolsky SA, Vettering WT (1989) Numerical recipes in Pascal: the art of scientific computing. Cambridge University Press, Cambridge, UK

Rissing SW, Pollock GB (1987) Queen aggression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). Anim Behav 35: 975–981

Rissing SW, Pollock GB (1991) An experimental analysis of pleometrotic advantage in the desert seed-harvester ant *Messor pergandei* (Hymenoptera : Formicidae). Insectes Soc 38: 205–211

Ross KG, Fletcher DJC (1985a) Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera : Formicidae). Behav Ecol Sociobiol 17: 349–356

Ross KG, Fletcher DJC (1985b) Genetic origin of male diploidy in the fire ant, *Solenopsis invicta* (Hymenoptera : Formicidae), and its evolutionary significance. Evolution 39: 888–903

Ryti RT (1991) Theoretical considerations of density-dependent spacing of a mound-building ant (*Formica altipetens*). J Theor Biol 147: 289–301

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

Ryti RT, Case TJ (1988) The regeneration niche of desert ants: effects of established colonies. Oecologia 75: 303–306

Ryti RT, Case TJ (1992) The role of neighborhood competition in the spacing and diversity of ant communities. Am Nat 139: 355–374

Slatkin M, Anderson DJ (1984) A model of competition for space. Ecology 65: 1840–1845

Tennant LE, Porter SD (1991) Comparison of diets of two fire ant species (Hymenoptera : Formicidae): solid and liquid components. J Entomol Sci 26: 450–465

Thurber DK, Bell MC, Black HL, Jorgensen CD (1993) Dispersion and mortality of colonies of the tropical ant *Paraponera clavata*. Biotropica 25: 215–221

Tschinkel WR (1992a) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. Ecol Entomol 17: 179–188

Tschinkel WR (1992b) Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera : Formicidae): laboratory and field observations. Ann Entomol Soc Am 85: 638–646

Tschinkel WR (1993) Resource allocation, brood production and cannibalism during colony foundation in the fire ant, *Solenopsis invicta*. Behav Ecol Sociobiol 33: 209–223

Tschinkel WR, Howard DF (1983) Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. Behav Ecol Sociobiol 12: 103–113

Vargo EL, Porter SD (1989) Colony reproduction by budding in the polygyne form of *Solenopsis invicta* (Hymenoptera: Formicidae). Ann Entomol Soc Am 82: 307–313

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

Weiner J (1985) Size hierarchies in experimental populations of annual plants. Ecology 66: 743–752

Wilson NL, Dillier JH, Markin GP (1971) Foraging territories of imported fire ants. Ann Entomol Soc Am 64: 660–665

Wood TG, Lee KE (1971) Abundance of mounds and competition among colonies of some Australian termite species. Pedobiologia 11: 341–366

Yodzis P (1978) Competition for space and the structure of ecological communities. Springer, Berlin Heidelberg New York