WILEY

British Ecological Society

Density-dependent competition in fire ants: effects on colony survivorship and size variation

ELDRIDGE S. ADAMS and WALTER R. TSCHINKEL

Department of Biology, University of Rochester, Rochester, NY 14627, USA; and Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA

Summary

1. Competition among ants can drive changes in both the density and the sizes of colonies. Models of competitive interactions produce conflicting predictions concerning size variation; these predictions have not previously been tested in social insect populations.

2. To measure the effects of early competition on population dynamics of the fire ant *Solenopsis invicta*, 2284 incipient colonies, each grown from a single queen, were planted in replicate arrays in an irrigated field. In a series of three experiments, colonies were planted in square grids with either 13·5, 15, 40, 60 or 120 cm between nearest neighbours.

3. Soon after planting, active colonies organized brood raids, which ended when victorious colonies acquired the brood and workers of one or more neighbours.

4. Initial colony density had strong effects upon the percentage of colonies engaged in raids, which ranged from 0% at the lowest density to 68·5% at the highest density. High colony density markedly increased raid complexity, colony mortality and queen migration.

5. The complex brood raids seen at high colony density rapidly reorganized clusters of incipient colonies. Excavation of surviving colonies showed that the number of workers per colony was more variable on plots with numerous raids; thus, competition by brood raiding tended to increase the degree of size inequality among colonies. This result is consistent with models and observations of 'asymmetric competition' among sessile organisms.

6. During raids, queens sometimes moved to nearby nests where they joined or usurped the original queen. Queen usurpation was especially likely on high-density plots.

7. Brood raids were restricted to the first few weeks following worker emergence and were reduced by low surface moisture, apparently because worker activity declines in dry conditions. By 10 weeks following emergence, the ants developed intolerance of workers from neighbouring colonies, and the mechanism of competition changed from brood raids to group fighting at food resources or foraging trails.

Key-words: brood raids, Formicidae, population dynamics, *Solenopsis invicta*.

Journal of Animal Ecology (1995) **64**, 315–324

Introduction

Competition among colonies is frequently reported within ant populations (Hölldobler & Wilson 1990). While the behavioural mechanisms of competition have been documented in detail for many species of ants (e.g. Hölldobler 1976, 1981; Traniello 1983; Adams 1990, 1994), the effects of competition on population dynamics in the social insects are poorly understood. Only a small number of field studies has gathered longitudinal data on colony densities and sizes (e.g. Brian & Elmes 1974).

A population of ants can be described by the densities, positions and sizes of colonies. Local competitive interactions can lead to a reduction of colony density or to changes in spatial pattern if colonies are killed (Hölldobler 1976) or forced to relocate (De Vita 1979). Competition can also change the size distributions of colonies if competing colonies affect one another's growth (Pontin 1961). While colony density or spatial

pattern are often reported in studies on ants (e.g. Davidson 1985; Ryti & Case 1986), the effects of competition on colony sizes have received much less attention (but see Pontin 1961; Ryti & Case 1992). Size variation is of considerable importance in ant population dynamics. Within a population, mature colony size, measured by the number of workers or by the biomass of ants, may vary over two orders of magnitude or more (Brian & Elmes 1974; Tschinkel 1993). Across this large range, colony size has strong effects on success in competitive struggles (e.g. Adams 1990), colony growth rates (e.g. Tschinkel 1993) and rates of reproduction (e.g. Brian & Elmes 1974; Tschinkel 1993). Furthermore, the size structure of a population reflects the partitioning of resources, which can affect the stability of population dynamics (Wall & Begon 1987; Lomnicki 1988). Yet, to our knowledge, no study has examined experimentally how competition among colonies affects the size distributions of survivors.

There has been considerable controversy over the effects of competition on size variation in other taxa. Three models can be distinguished. These models were developed originally for solitary or modular organisms (Harper 1981), but may also be applied to social insects if one recognizes that the competing 'individuals' are whole colonies. First, the 'resource depletion model' (Weiner & Thomas 1986) predicts that size variation will be reduced or unaffected by competition. Under this model, size inequalities increase with time, even in the absence of competition, due to variation in growth rates resulting from a variety of genetic and environmental influences (Koyama & Kira 1956; Benjamin & Hardwick 1986). If competition broadly reduces the growth rates of all individuals, this can reduce the rate at which size inequalities develop (Turner & Rabinowitz 1983; Weiner & Thomas 1986). Secondly, the 'asymmetric competition' or 'dominance and suppression' model (Weiner 1985; Weiner & Thomas 1986) predicts that populations grown at higher densities will show greater size variation due to the differential success of larger competitors. Under this hypothesis, large individuals (or colonies) suppress the growth of small individuals more than they are suppressed in return. Competition thus tends to exaggerate the degree of size variation within the population. This model is supported by numerous experimental studies on plants (reviewed by Weiner & Thomas 1986) and animals (Wall & Begon 1987; Ellison & Harvell 1989). Miller & Weiner (1989) and Bonan (1991) have shown that symmetric, as well as asymmetric, competition can exaggerate size inequalities if there is local variation in spatial pattern. Thirdly, the 'size truncation model' applies when competition results in the death of the smallest individuals or colonies. The loss of the smallest competitors reduces the range of sizes and therefore lowers the degree of size variation (Weiner & Thomas 1986; Wall & Begon 1987). It should be noted that these three models are not mutually exclusive. For example, asymmetric competition in populations of plants can lead to increased size inequalities prior to the onset of mortality, then to declining inequalities as the smallest individuals die (Weiner & Thomas 1986).

This paper introduces a method for the study of density-dependent competition in populations of ants. Assemblages of incipient colonies of the fire ant *Solenopsis invicta* Buren were planted at various densities and monitored to quantify the effects of competition upon colony survivorship and size variation. Young colonies of the monogyne form of *S. invicta* compete by brood raids, in which the workers and brood of losing colonies are acquired by winning colonies (Stamps & Vinson 1991; Tschinkel 1992a,b). This form of competition has also been documented among incipient colonies of the honey ant *Myrmecocystus mimicus* Wheeler (Bartz & Hölldobler 1982) and the harvester ant *Messor* (= *Veromessor*) *pergandei* Mayr (Rissing & Pollock 1987, 1991), and among mature colonies of *M. mimicus* (Hölldobler 1981). Most studies of brood raids have been conducted in the laboratory, but Tschinkel (1992a) showed that a majority of incipient colonies of *S. invicta* in a field population engaged in raids and that raids were the primary source of mortality during the first few weeks following worker emergence. In this study, experimental plantings were used to quantify the effects of initial colony density on the process of brood raiding and to test whether early competition increases the degree of size inequality among surviving colonies.

Materials and methods

FIRE ANT BACKGROUND

The fire ant *S. invicta* occurs in high densities in many parts of the southeastern United States, where it has spread following introduction from South America (Lofgren 1986). Details of the behaviour of brood raiding are described by Tschinkel (1992a,b) and by Stamps & Vinson (1991). Brood raids are organized struggles in which workers retrieve immature ants (eggs, larvae, pupae, or callow workers) from nearby colonies to be reared within the raiding nests. Upon maturation, the captured ants labour within the host colony, thereby supplementing its population of sterile workers. In an extreme case, one complex brood raid involved at least 80 colonies, of which only two survived (Tschinkel 1992b).

Two social forms of *S. invicta* have been discovered in the United States since its introduction from South America (Ross & Fletcher 1985a). This paper concerns only the monogyne form, which is the only form known from Leon County, Florida (Porter 1992; W. Tschinkel, personal observations). Mature colonies of the monogyne form contain a single egg-laying queen, are mutually intolerant, and defend discrete foraging

territories (Wilson, Dillier & Markin 1971; Ross & Fletcher 1985a; Showler, Knaus & Reagan 1990). Colonies are founded by single queens or by small groups of co-operating queens shortly after mating flights (Tschinkel & Howard 1983). Queens found nests claustrally by digging small chambers in the soil, depositing eggs, and rearing the first cohort of workers using stored reserves (Markin, Collins & Dillier 1972). The first workers, called 'minims,' are unusually small (Porter & Tschinkel 1987). Although co-operative nest founding is common, only a single queen will survive within each nest due to fighting among the queens and to executions by the workers (Markin *et al.* 1972).

COLLECTION AND REARING OF QUEENS

Queens were collected in Tallahassee, Florida, within hours following large nuptial flights. After mating aerially, queens land, drop their wings, and search for sites to found a colony (Markin *et al.* 1972). They can be gathered easily on parking lots, where they cannot excavate chambers and accumulate instead along curbs and beneath objects that provide shade or moisture.

Queens were maintained individually in the laboratory until their first workers eclosed. Queens were kept without food in moist plaster nests or in test tubes provided with moist cotton. Colonies were selected for planting on the basis of health and the number of pupae and workers. Queens that died, laid eggs which failed to develop, produced diploid males (Ross & Fletcher 1985b), or produced unusually small broods were rejected.

Each colony was transferred to an artificial nest. The artificial nests were plaster blocks, measuring approximately $5 \times 2 \times 2$ 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. Queens and their offspring were chilled to induce temporary torpor, then aspirated into the plaster nest. Each nest was wrapped temporarily in toilet paper to prevent escape by the workers or queens during transport to the field.

PREPARATION OF FIELD SITES

Fieldwork was conducted at the Mission Road Biological Station of Florida State University in Tallahassee, Florida. Colonies were planted in an unshaded spray-irrigated field, from which existing colonies of fire ants were first removed in two phases. Two months prior to planting, the pesticide Amdro (American Cyanamid, Princeton, New Jersey, USA) was broadcast over the experimental area and at least 20 m beyond in each direction. This pesticide breaks down quickly in sunlight or water, and leaves no detectable toxic residue after several days (Apperson, Leidy & Powell 1984). When necessary, colony removals were completed by driving a stake deeply into the nest

several times and by filling the resulting holes with boiling water. The effectiveness of removal was confirmed by placing transects of baits across the field.

Prior to each experiment, the field was tilled, flattened, and raked to reduce weeds and to homogenize the conditions across all replicate plots. In experiments 2 and 3, the plots were watered as necessary to maintain surface soil moisture.

Each plot consisted of a square grid of nest sites. The distance between rows and columns of the grid was varied as described below. Each nest site was marked with a 12-cm wooden marker and a 4×4 cm metal tag held in place by a nail. This allowed rapid surveys of colony entrances, which are small and would otherwise be difficult to locate.

Adjacent grids were at least 5 m apart, which was far enough to prevent raids between neighbouring plots. In addition, a border of at least 5 m around the experimental sites was tilled or mowed to reduce vegetation cover. This allowed easy observation of raids and other ant activity near each plot, which was necessary for documenting colony survivorship and for detecting any naturally occurring colonies.

To plant each colony, a narrow hole 7 cm deep was prepared at the marked nest site. This mimics the natural depth of incipient nest chambers (W. Tschinkel, unpublished data). The paper covering of each plaster nest was removed, and the plaster nest with its incipient colony was inserted into the hole so that the large chamber was at the bottom. Each nest was then covered with soil.

Despite the initial removals, some 'wild' ant colonies became established near our experimentally planted colonies due to naturally occurring nuptial flights or, less frequently, to migration of mature colonies from surrounding areas. These colonies were removed by excavation or by soaking with boiling water.

EXPERIMENT DESIGN

Three experiments were conducted sequentially, each with a high-density treatment and a low-density treatment. The methods were refined on the basis of each set of results. Nearest neighbour distances in naturally established incipient fire ant colonies near the study site ranged from 8 cm to 2·04 m (W. Tschinkel, personal observations). For each experiment, distances between planted colonies were selected from within this range, so that collectively the treatments spanned most of the range of natural variation in colony spacing. In each experiment, the distance between nearest neighbours differed by a factor of three or four between the high- and low-density treatments, producing a strong contrast in density. Colonies were randomly assigned to treatment.

Experiment 1 (120 vs. 40 cm)

Colonies selected for planting contained between 5 and 20 minims (mean$\pm$SE: $10·16\pm1·54$). Colonies

were planted in assemblages of 144, arranged in square grids of 12×12. In the high-density treatment, nearest neighbours were separated by 40 cm; in the low-density treatment, by 1·2 m. Four high-density plots and two low-density plots were planted from 5 July to 8 July 1990. Treatments were randomly assigned to available sites. Two additional high-density and three new low-density plots were planted between 14 August and 19 August 1990. The difference in starting dates was due to the need for further efforts to remove mature colonies at some locations. Preliminary statistical tests showed no significant effect of planting date on brood raids or colony survivorship, so data from the two planting dates were lumped together. The plots were not watered, but were exposed to natural rainfall. All plots were surveyed every other day for 55 days. From 37 to 41 days after planting, several randomly selected colonies were excavated and censused.

Experiment 2 (40 vs. 13·3 cm)

In the second experiment, colonies were planted in assemblages of 25 arranged in a 5×5 square grid (Fig. 1). As in experiment 1, colonies selected for planting contained between 5 and 20 minims. High-density colonies were separated by 13·3 cm from their nearest neighbours, low-density colonies by 40 cm. Six replicate plots at each density were planted on 24 and 25 September 1990. Treatments were assigned randomly to available sites. Because the soil was initially nearly free of vegetation, food was supplemented by placing fragments of dead crickets and cotton moistened with dilute honey in front of each colony's entrance. Colonies were fed twice per week during the first 2 weeks, after which new vegetation and associated insects provided reliable sources of food. Colonies were censused for activity daily for 17 days, then at least once every other day until 30 October, 1990.

Experiment 3 (60 vs. 15 cm)

For the third experiment, assemblages of 25 colonies were planted in square grids of 5×5. Colonies were separated from nearest neighbours by 15 cm in high-density plots and by 60 cm on low-density plots. One goal of this experiment was to assess the effects of colony density on the sizes (worker number) of surviving colonies; therefore, each colony was censused within 24 h before planting. Colonies selected for planting contained from 4 to 15 eclosed workers and from 8 to 30 pupae. Six pairs of high- and low-density plots were planted between 3 July and 16 July 1991, each pair matched for date of planting and for east–west location within the irrigated field. For each pair of plots, 50 incipient colonies were randomly assigned to treatment. Each queen was marked on the sides of the thorax with a unique combination of coloured paints. No effect of paint on queen survivorship or on worker acceptance of queens has been detected (E. Adams, unpublished data).

Colonies were excavated after brood raiding on high-density plots had ceased or had peaked and then declined to include less than 8% of colonies per day. This occurred 3–9 days after planting. Plots were excavated in pairs, so that equal numbers of high- and low-density plots were excavated each day. All colonies were excavated on high-density plots. Randomly selected surviving colonies were excavated on low-density plots until at least five colonies per plot had been harvested. In most cases, excavations revealed one or two chambers containing the workers, brood and queen. In one high-density plot, the queen and brood chamber of the sole surviving colony could not be found; therefore, this plot and its paired low-density plot were omitted from statistical tests requiring complete colony census.

SAMPLING OF COLONY ACTIVITY

Previous work has shown that most brood raids occur during the morning and evening and that most raids are more than 30 min duration (Tschinkel 1992a). In experiment 1, colonies were surveyed every other day between 8.00 and 10.30 AM depending on weather, so that surveys were conducted during periods of peak activity. In experiment 3 and during the first 8 days of experiment 2, surveys were increased to approximately once per hour every day during the morning and evening hours to record foraging activity and brood raids. Each colony was visited at least four times each morning (8.00 AM to 1.00 PM) and at least once each evening (6.30 to 7.30 PM), except during heavy rains. When brood raids were observed, additional surveys were added for all plots to assure a high probability of recording brood raids and to resolve the pattern of movement between neighbouring colonies.

During each survey, we recorded whether the colony had an open entrance and whether ants were active at the entrance. Whenever brood raids were seen, the pathways used by ants to travel from one colony to another were recorded, as well as the origin and destination of any workers carrying brood. When queens were seen on the surface of the soil, their colour marks, if any, were recorded and their movements and interactions were noted.

STATISTICAL ANALYSIS

At each census, colonies were judged to be active if an entrance hole was seen at the marked location. Excavation of colonies has shown that not all apparent entrance holes are associated with live colonies (E. Adams, unpublished data). Records for individual colonies in experiment 1 sometimes showed a series of nine or more sequential observations of inactivity

followed by one or a few later records of apparent entrances. If no ants were seen during these later records, they were disregarded to avoid over-estimating colony longevity. To improve further the accuracy of survivorship estimates, the frequency of censuses increased from experiment 1 to 3 (see above). In addition, in experiments 2 and 3, entrance holes were sealed with moist soil at the end of each day. Active colonies quickly excavated through the plug, while entrance holes for dead or abandoned colonies remained plugged and were no longer counted.

Many familiar methods for analysis of survivorship data assume that deaths are independent of one another. Since this assumption is clearly violated in a population with frequent brood raids, these methods were not appropriate. Instead, a single statistic was calculated for each plot—the median date of colony death. Median dates of death for plots planted at different densities were compared by the Mann-Whitney U-test. Since colonies in experiment 3 were excavated a few days after planting, no analysis of colony survivorship was conducted.

Colonies in the interior of a plot have more neighbours than do those on the outermost edge. To test whether position within the plot affected colony fate, each plot was divided into two sections, one composed of colonies on the outermost edge of planted sites and the other composed of colonies in the interior. The proportions of colonies engaging in raids and the median lengths of colony survival were compared.

Several statistics have been used to quantify size inequalities, including the Gini coefficient, measures of skewness, and the coefficient of variation (Benjamin & Hardwick 1986; Bendel *et al.* 1989). Bendel *et al.* (1989) compare the performance of these statistics and show that the coefficient of variation is particularly sensitive to the right tail of the distribution of sizes. Since we were especially concerned with detecting the presence of unusually large colonies, we used the coefficient of variation instead of alternative measurements.

Results

EXPERIMENT 1

Colony density had no significant effect on the proportion of colonies surviving planting or on subsequent colony survival. The only raids ($n = 33$) were on high-density plots (40 cm between neighbours), but the proportion of colonies engaging in raids did not vary significantly with density (Table 1). Raids occurred between 2 and 8 days after planting, with a median of 3 days.

The degree of raiding within high-density plots was variable. In the extreme case, 35 colonies engaged in raids on a single plot, accounting for 25·7% of colonies that survived planting. By contrast, no raids were seen in three plots planted at the same density,

and only small numbers of raids (three or four) were seen on the two remaining replicates. This variation may have been due to soil moisture, which was determined primarily by the uncontrolled pattern of rainfall with respect to planting dates. To reduce this source of variation in subsequent experiments, all plots were watered on each day for which there was no natural rainfall.

Two plots were monitored in detail for 73 days. By 66 days after planting, surviving colonies had begun to form semipermanent foraging tunnels characteristic of mature nests. These led outward underground from the central nest site; some were more than 2 m in length. By this age, competitive encounters had shifted from brood raiding to territory defence. Workers from differing colonies on the same plot fought spontaneously when they encountered one another during foraging, and fights between colonies were readily induced by placing baits at intermediate positions. Fighting colonies recruited up to 140 workers during battles for food baits, but these struggles did not end in brood raids ($n = 9$).

Thirteen randomly selected live colonies were excavated between 37 and 41 days after planting. A single queen was recovered from 11 of these colonies; no queen was found in the remaining two. Colony sizes were highly variable, with an average of $109·9 \pm 34·0$ workers (mean $\pm$ SE; range 5–342) and $228·9 \pm 82·8$ immature ants (range 1–820).
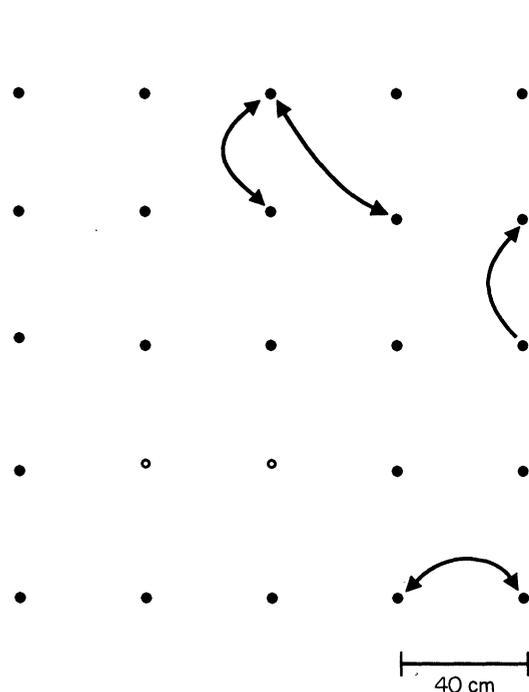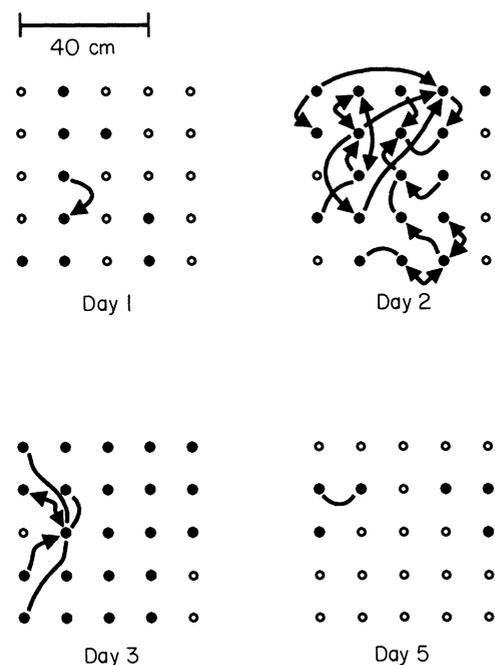
EXPERIMENT 2

Colony density did not affect the proportion of colonies that survived planting (Table 1). Density had a strong and significant positive effect upon the proportion of colonies that engaged in raids and the average number of raid partners for colonies that participated in raids. It had a negative effect on the median date of colony death. Raids on typical high- and low-density plots are illustrated in Figs 1 and 2. Raids occurred from 2 to 8 days after planting on low-density plots (median = 5 days) and from 1 to 5 days after planting on high-density plots (median = 2 days). Average survivorship curves for high- and low-density plots are shown in Fig. 3.

EXPERIMENT 3

As in the previous experiments, colony density had no effect on the proportion of colonies that survived planting. Density had strong positive effects on the number and complexity of raids. On low-density plots (60 cm between neighbours), few colonies engaged in raids, and all raids involved only a single pair of colonies. On high-density plots (15 cm between neighbours), most colonies engaged in raids and these colonies interacted on average with more than two competitors (Table 1). Raids occurred from 1 to 6 days after planting on low-density plots (median = 2 days)

Table 1. Average values (mean ± SE) of colony and population characteristics for assemblages of incipient colonies planted at various densities. For colonies that participated in raids, the average number of other colonies with which workers or brood were exchanged ('raid partners') is given. *P* values are for the Mann-Whitney *U*-test

	Low density	High density	*P*
Experiment 1			
Distance between nearest neighbours	120 cm	40 cm	
Number of replicate plots	5	6	
Percentage colonies surviving planting	86·1 ± 2·9	91·9 ± 2·0	NS
Percentage colonies involved in raids	0 ± 0	5·12 ± 4·2	NS
Average number of raid partners	None	1·33 ± 0·19	
Median life span of colony (days)	16·6 ± 2·7	17·2 ± 3·2	NS
Experiment 2			
Distance between nearest neighbours	40 cm	13·3 cm	
Number of replicate plots	6	6	
Percentage colonies surviving planting	96·0 ± 1·5	96·0 ± 1·8	NS
Percentage colonies involved in raids	21·7 ± 4·7	68·5 ± 6·3	<0·01
Average number of raid partners	1·22 ± 0·13	2·06 ± 0·15	<0·01
Median life span of colony (days)	21·7 ± 1·9	6·2 ± 0·3	<0·01
Experiment 3			
Distance between nearest neighbours	60 cm	15 cm	
Number of replicate plots	8	8	
Percentage colonies surviving planting	94·0 ± 2·0	94·0 ± 1·7	NS
Percentage colonies involved in raids	7·6 ± 2·0	68·2 ± 4·6	<0·01
Average number of raid partners	1·0 ± 0	2·21 ± 0·17	<0·01
Percentage queens seen on surface	1·5 ± 0·01	15·0 ± 0·10	<0·01
At time of planting			
Workers per colony	7·46 ± 0·30	7·82 ± 0·41	NS
Coefficient of variation	0·300 ± 0·018	0·263 ± 0·020	NS
At harvest			
Workers per surviving colony	14·1 ± 0·82	21·4 ± 3·98	NS
Coefficient of variation	0·56 ± 0·06	1·47 ± 0·31	<0·005

Fig. 1. Cumulative map of brood raids on a representative low-density plot. Lines connect colonies between which raiding workers moved; arrows indicate the direction of movement of workers carrying brood. Solid circles indicate planted colonies that survived planting; open circles indicate colonies that never showed activity.

Fig. 2. Sequential maps of brood raids on a representative high-density plot. Lines connect colonies between which raiding workers moved; arrows indicate the direction of movement of workers carrying brood. Lines without arrows indicate worker traffic without transport of brood. Solid circles indicate colonies active on each illustrated day. No raids were seen on the fourth day.
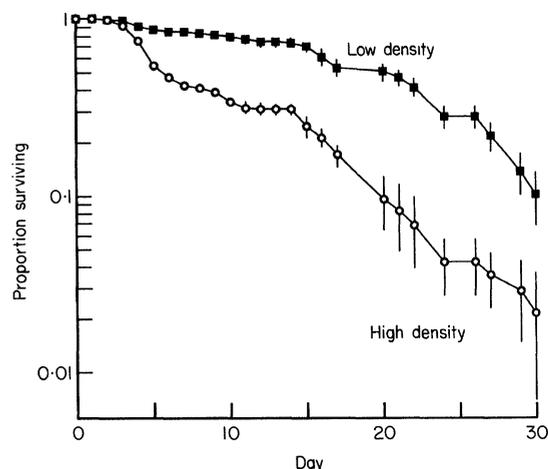
Fig. 3. Mean survivorship ($\pm$ SE) for colonies planted at high density (open circles; six plots planted with 13·3-cm spacing) and low density (solid squares; six plots planted with 40-cm spacing).

and from 1 to 7 days after planting on high-density plots (median = 2 days).

Queens occasionally emerged to the surface of the soil during or shortly after raids. Paint marks on the thoraxes confirmed that these were queens planted in incipient colonies and allowed identification of the origin of each queen. Significantly more migrating queens were seen on high-density plots than on low-density plots (Table 1). Many queens tried to enter other colonies, but were often resisted by workers. Some queens successfully entered colonies; many of these emerged a short time later. A single detailed example is provided below.

A queen identified by yellow paint on both sides of her thorax (queen YY) was planted in position 25 of a high-density plot (15 cm between neighbours) on the morning of 16 July 1991. This colony was raided by colony 22 at 9.44 AM on 19 July. At 10.07 AM, queen YY was seen digging into the entrance of colony 22 under attack by two workers, which grasped her by the legs. She left this entrance and dug at the entrance of colony 21 at 11.51 AM. During the same morning, five other colonies participated in raids on this plot and three other marked queens were seen moving among colony entrances. Queen YY was not seen again on the surface, but was recovered alive, along with 67 workers, during the excavation of nest 13 on 21 July, at which time she was the sole queen in this nest.

When colonies were excavated, live or dead queens were recovered at a majority of nests with open entrances. Of those sites with live queens, 90·7% ($n = 43$) of nests on low-density plots contained only the original queen, while only 69·6% ($n = 46$) of nests on high-density plots contained only the original queen ($P < 0.02$, G-test). The exceptions included 14 colonies in which the original queen had been replaced by a queen originally planted at a different nest site, and four colonies in which both the original queen

and one or more other queens were recovered alive at the same nest site.

The assemblages of colonies planted in high- and low-density plots did not differ initially in average worker number or in the degree of size inequality. During the first few days of growth and interaction, the mean and the coefficients of variation of worker number rose on both high- and low-density plots; however, the degree of increase was greater on high-density plots. At the time of harvest, the variation in worker number among surviving colonies was significantly greater on high-density plots than on low-density plots (Table 1).

EDGE EFFECTS

Within plots planted at the highest density (13·3 cm between nearest neighbours; experiment 2), the percentage of colonies engaging in raids was significantly higher in the interior of each planted grid ($82·9 \pm 4·9\%$) than on the edge ($60·1 \pm 7·2\%$; $P < 0.05$, Mann-Whitney U-test). In addition, the median length of colony survival was significantly lower in the interior of the plot than on the edge ($5·33 \pm 0·37$ vs. $7·17 \pm 0·70$ days; $P < 0.05$, Mann-Whitney U-test). No significant edge effects were found for any other planting density.

Discussion

The results of these experiments show that early competition among colonies is density-dependent and asymmetric. The frequency and complexity of raids is governed by the probability of encounter among incipient colonies. Except at the lowest densities, the proportion of colonies engaged in raids increased with colony density (Table 1). Brood raids reduced colony survivorship (Fig. 3) and increased rates of queen migration and usurpation (Table 1). In the literature on population ecology, competition is said to be asymmetric when larger individuals gain a share of contested resources that is greater than their relative mass (Begon 1984; Weiner & Thomas 1986). Game theoretical studies of animal aggression describe other kinds of differences between competitors as 'asymmetries', but we use the more restrictive definition in this paper. Brood raiding is asymmetric in that larger colonies are more likely to win and the winning colony acquires essentially all of the brood and workers of the losing colony (Tschinkel 1992b). Although brood raids could conceivably lower the degree of size variation among surviving colonies by eliminating the smallest competitors, in agreement with the size truncation model, this study shows that the net effect of brood raids is to increase size inequalities by concentrating many of the workers from unsuccessful colonies within a few victorious colonies.

Brood raids can lead to the rapid growth of winning colonies within dense populations. In this study, the

winning colonies in crowded populations grew faster by accumulation of brood than colonies that escaped competition. This same phenomenon has been reported in natural populations, where some raiding colonies acquire more than 1000 workers within a few weeks (Tschinkel 1992b), many times the number produced by queens founding colonies in isolation. Thus, dense populations of colonies quickly develop marked discrepancies in size, which are likely to affect their fates over the subsequent months or years. Moreover, the victorious colonies in crowded populations actually benefit by raiding even though the average effect of brood raids on young colonies is detrimental. Such an effect is unlikely to occur in populations of competing plants, or other sessile organisms, since there is generally no mechanism by which successful plants acquire resources stored by their competitors. The accumulation of brood or workers within victorious colonies occurs in other brood-raiding ants, both in incipient stages (Bartz & Hölldobler 1982; Rissing & Pollock 1987, 1991) and in mature colonies (Hölldobler 1981; Stuart & Alloway 1982), underscoring the similarities between brood raids and some forms of interspecific parasitism (Wilson 1975; Alloway 1980; Pollock & Rissing 1989).

The tendency of competition to exaggerate size inequalities may not persist in older populations. Brood raiding is a temporary phenomenon, confined to the first few days or weeks of activity. Workers in incipient colonies often tolerate non-nestmates and can join with them into a single nest site. By contrast, workers from older colonies are mutually intolerant, defend territories, and cannot be mixed without substantial worker mortality (Wilson *et al.* 1971; Showler *et al.* 1990). It is likely that this ontogenetic switch in aggressive behaviour changes the rules of population dynamics. Once territory defence begins, the accumulation of workers and brood into the nests of superior competitors ceases; instead, it is likely that every colony's growth is suppressed in crowded populations, although the degree of suppression may be greater for smaller colonies. Furthermore, colonies of *S. invicta* show sigmoidal growth patterns, so that relative growth rates decline as colonies approach their maximum size (Tschinkel 1993). Thus, growth rates are positively correlated with size for the youngest colonies, but negatively correlated with size for the largest mature colonies. A negative correlation between size and growth rates should cause size inequalities to decrease with time (Westoby 1982; Hara 1984; Bonan 1988); however, the effects of territorial competition on population-wide size distributions have yet to be measured.

Many previous studies of ant populations have detected population-level effects of competition by less direct methods. The most commonly used techniques are passive statistical analyses, which infer competition from the dispersion of colony locations (reviewed by Levings & Traniello 1981) or from other patterns of density, size and dispersion (e.g. Waloff & Blackith 1962; Cushman, Martinsen & Mazeroll 1988). Experimental studies are also common, but most are removals of mature colonies (Hölldobler & Wilson 1990). Few, if any, of these experiments address the effects of intraspecific competition upon population-wide patterns of growth and survivorship. Observational studies following populations across time document survivorship and may indicate the causes of mortality (e.g. Fowler 1987; Tschinkel 1992a). To our knowledge, this is the first study to employ experimental planting of incipient ant colonies as a method for measuring the effects of colony density on competition. This method allows a high degree of control over the contents of each colony, the spatial arrangement of colonies, the timing of planting, and many physical aspects of the habitat.

The density of colonies in our high-density treatments was within the range of natural densities (W. Tschinkel, personal observations). Furthermore, the number and complexity of raids seen within these assemblages was matched, and even surpassed, in naturally established populations (Tschinkel 1992a,b). However, colonies in our experimental plots did not appear to raid as frequently as colonies in natural populations at similar densities. This suggests that variables other than density affect the likelihood of raids. In this study, each planted colony contained a single queen and her progeny, but naturally established colonies may be founded by two or more queens, thereby increasing the number of workers that are produced in the first cohort (Tschinkel & Howard 1983). If larger colonies raid more frequently or over greater distances, then field populations may show higher frequencies of raids at lower densities than those adopted in our experiments.

Surface soil moisture appeared to affect the rate of raiding. This was suggested by the variation in rate of raiding on plots with 40 cm spacing between nearest neighbours. Of the six plots planted at this density in experiment 1, one replicate showed substantially more raiding than the others. This plot had been planted following a heavy rain which left the soil wet for several days, during which the raids occurred. This result prompted a change in experimental methods. In experiments 2 and 3, each plot was watered daily so that the soil surface was kept moist for all replicates. Under these conditions, plots planted with 40 cm between neighbours showed higher levels of raiding than in experiment 1. The effect of soil moisture is probably due more to desiccation stress than to softening of the soil, since raiding workers do not need to excavate soil in order to obtain brood. Fire ant activity is sensitive to microclimate (Porter & Tschinkel 1987). Hot dry conditions may diminish ant activity, and thereby reduce the probability that workers discover nearby colonies and initiate brood raids. We hypothesize that the frequency and complexity of raids is determined by the probability of encounters between

colonies, which is in turn affected by colony size, spacing and activity.

References

Adams, E.S. (1990) Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Animal Behaviour*, **39**, 321–328.

Adams, E.S. (1994) Territory defense by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic. *Oecologia*, **97**, 202–208.

Alloway, T.M. (1980) The origins of slavery in leptothoracine ants (Hymenoptera: Formicidae). *American Naturalist*, **115**, 247–261.

Apperson, C.S., Leidy, R.B. & Powell, E.E. (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. *Journal of Economic Entomology*, **77**, 1012–1018.

Bartz, S.H. & Hölldobler, B. (1982) Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behavioral Ecology and Sociobiology*, **10**, 137–147.

Begon, M. (1984) Density and individual fitness: asymmetric competition. *Evolutionary Ecology* (ed. B. Shorrocks), pp. 175–194. Blackwell, Oxford.

Bendel, R.B., Higgins, S.S., Teberg, J.E. & Pyke, D.A. (1989) Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. *Oecologia*, **78**, 394–400.

Benjamin, L.R. & Hardwick, R.C. (1986) Sources of variation and measures of variability in even-aged stands of plants. *Annals of Botany*, **58**, 757–778.

Brian, M.V. & Elmes, G.W. (1974) Production by the ant *Tetramorium caespitum* in a southern English heath. *Journal of Animal Ecology*, **43**, 889–903.

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

Bonan, G.B. (1991) Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Annals of Botany*, **68**, 341–347.

Cushman, J.H., Martinsen, G.D. & Mazeroll, A.I. (1988) Density- and size-dependent spacing of ant nests: evidence for intraspecific competition. *Oecologia*, **77**, 522–525.

Davidson, D.W. (1985) An experimental study of diffuse competition in harvester ants. *American Naturalist*, **125**, 500–506.

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.

Ellison, A.M. & Harvell, C.D. (1989) Size hierarchies in *Membranipora membranacea*: do colonial animals follow the same rules as plants? *Oikos*, **55**, 349–355.

Fowler, H.G. (1987) Colonization patterns of the leaf-cutting ant, *Atta bisphaerica* Forel: evidence for population regulation. *Journal of Applied Entomology*, **104**, 102–105.

Hara, T. (1984) Dynamics of stand structure in plant monocultures. *Journal of Theoretical Biology*, **110**, 223–239.

Harper, J.L. (1981) The concept of population in modular organisms. *Theoretical Ecology: Principles and Applications* (ed. R.M. May), 2nd edn, pp. 53–77. Sinauer, Sunderland, Massachusetts.

Hölldobler, B. (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology*, **1**, 3–44.

Hölldobler, B. (1981) Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **9**, 301–314.

Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap Press of Harvard University, Cambridge, Massachusetts.

Koyama, H. & Kira, T. (1956) Intraspecific competition among higher plants. VIII. Frequency distributions of individual plant weight as affected by the interaction between plants. *Journal of the Institute of Polytechnics, Osaka City University Series D*, **7**, 73–94.

Levings, S.C. & Traniello, J.F.A. (1981) Territoriality, nest dispersion, and community structure in ants. *Psyche*, **88**, 265–319.

Lofgren, C.S. (1986) History of imported fire ants in the United States. *Fire Ants and Leaf-Cutting Ants: Biology and Management* (eds C.S. Lofgren & R.K. Vander Meer), pp. 36–47. Westview Press, Boulder, Colorado.

Lomnicki, A. (1988) *Population Ecology of Individuals*. Princeton University Press, Princeton, New Jersey.

Markin, G.P., Collins, H.L. & Dillier, J.H. (1972) Colony founding by queens of the red imported fire ant, *Solenopsis invicta*. *Annals of the Entomological Society of America*, **65**, 1053–1058.

Miller, T.E. & Weiner, J. (1989) Local density variation may mimic effects of asymmetric competition on plant size variability. *Ecology*, **70**, 1188–1191.

Pollock, G.B. & Rissing, S.W. (1989) Intraspecific brood raiding, territoriality, and slavery in ants. *American Naturalist*, **133**, 61–70.

Pontin, A.J. (1961) Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). *Journal of Animal Ecology*, **30**, 47–54.

Porter, S.D. (1992) Frequency and distribution of polygyne fire ants (Hymenoptera: Formicidae) in Florida. *Florida Entomologist*, **75**, 248–257.

Porter, S.D. & Tschinkel, W.R. (1987) Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environmental Entomology*, **16**, 802–808.

Rissing, S.W. & Pollock, G.B. (1987) Queen aggression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Animal Behaviour*, **35**, 975–981.

Rissing, S.W. & Pollock, G.B. (1991) An experimental analysis of pleometrotic advantage in the desert seed-harvester ant *Messor pergandei* (Hymenoptera; Formicidae). *Insectes Sociaux*, **38**, 205–211.

Ross, K.G. & Fletcher, D.J.C. (1985a) Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **17**, 349–356.

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

Ryti, R.T. & Case, T.J. (1986) Overdispersion of ant colonies: a test of hypotheses. *Oecologia*, **69**, 446–453.

Ryti, R.T. & Case, T.J. (1992) The role of neighborhood competition in the spacing and diversity of ant communities. *American Naturalist*, **139**, 355–374.

Showler, A.T., Knaus, R.M. & Reagan, T.E. (1990) Studies of the territorial dynamics of the red imported fire and (*Solenopsis invicta* Buren, Hymenoptera: Formicidae). *Agriculture, Ecosystems and Environment*, **30**, 97–105.

Stamps, W.T. & Vinson, S.B. (1991) Raiding in newly founded colonies of *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Environmental Entomology*, **20**, 1037–1041.

Stuart, R.J. & Alloway, T.M. (1982) Territoriality and the origin of slave raiding in leptothoracine ants. *Science*, **215**, 1262–1263.

Traniello, J.F.A. (1983) Social organization and foraging success in *Lasius neoniger* (Hymenoptera: Formicidae): behavioral and ecological aspects of recruitment communication. *Oecologia*, **59**, 94–100.

Tschinkel, W.R. (1992a) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta. Ecological Entomology*, **17**, 179–188.

Tschinkel, W.R. (1992b) Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae): laboratory and field observations. *Annals of the Entomological Society of America*, **85**, 638–646.

Tschinkel, W.R. (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecological Monographs*, **63**, 425–457.

Tschinkel, W.R. & Howard, D.F. (1983) Colony founding by pleometrosis in the fire ant, *Solenopsis invicta. Behavioral Ecology and Sociobiology*, **12**, 103–113.

Turner, M.D. & Rabinowitz, D. (1983) Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa. Ecology*, **64**, 469–475.

Wall, R. & Begon, M. (1987) Individual variation and the effects of population density in the grasshopper *Chorthippus brunneus. Oikos*, **49**, 15–27.

Waloff, N. & Blackith, R.E. (1962) The growth and distribution of the mounds of *Lasius flavus* (Fabricius) (Hymenoptera: Formicidae) in Silwood Park, Berkshire. *Journal of Animal Ecology*, **31**, 421–437.

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

Weiner, J. & Thomas, S.C. (1986) Size variability and competition in plant monocultures. *Oikos*, **47**, 211–222.

Westoby, M. (1982) Frequency distributions of plant size during competitive growth of stands: the operation of distribution-modifying functions. *Annals of Botany*, **50**, 733–735.

Wilson, E.O. (1975) *Leptothorax duloticus* and the beginnings of slavery in ants. *Evolution*, **29**, 108–119.

Wilson, N.L., Dillier, J.H. & Markin, G.P. (1971) Foraging territories of imported fire ants. *Annals of the Entomological Society of America*, **64**, 660–665.