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What is the function of encounter patterns in ant colonies?

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Abstract. This study explores how patterns of brief antennal contacts may function in the organization of ant colonies. In the course of antennal contact, an ant can determine whether another is a nestmate. The first part of the work was comparative, and showed that three ant species (*Solenopsis invicta*, *Myrmica rubra*, and *Lasius fuliginosus*) differ in the frequency, location and context of antennal contact. The next part examined whether ants might use the rate of contacts with nestmates as a cue to nestmate density. Density was varied experimentally, and variation in contact rate was measured. If encounters between ants were the result of purely random collisions, the principles of Brownian motion suggest numbers of contacts would increase quadratically with numbers of ants. The results show that in undisturbed conditions, contact rate was not random. Instead ants (*L. fuliginosus*), regulated contact rate. Ants aggregated more when density was low, which keeps contact rate up, and avoided contact with nearby ants when density was high, which keeps contact rate low. One ant responds to another, and thus can decide whether to engage in contact, at a distance of 1·2 cm. Next, ants were exposed to workers from another colony. In these disturbed conditions, contact rates increased. The magnitude of the increase depended on proportions, not numbers of non-nestmates present, suggesting that contact rate may be a cue to nestmate density.

This study investigates the function of patterns of encounters in ant colonies. Such patterns are crucial to the organization of many vertebrate societies (e.g. Mitani et al. 1991), and may be important in social insects as well. Here we consider one type of encounter, brief antennal contact between two workers. Ants use their antennae in a variety of behavioural rituals (Lenoir & Jaisson 1982; Hölldobler 1984), but 'antennal contact', as used here, refers only to occasions when one ant briefly touches another's antennae with its own. Ants communicate using pheromones, which they perceive with their antennae. In the course of brief antennal contact, ants may receive chemical messages, such as that the individual being contacted is a nestmate.

In the first part of the study, we ask whether a pattern of antennal contact can be considered to be characteristic of the behaviour of an ant colony. To do this, we compare spatial and temporal patterns of antennal contact in three, ecologically very different species. The first, *Myrmica rubra*, has small colonies (with hundreds of workers) and its distribution tends to be limited by the presence of other species (Elmes & Wardlaw 1982). The second, the fire ant, *Solenopsis invicta* Buren, is an extremely effective competitor that thrives in disturbed habitats and has spread very rapidly across the southern U.S.A. since its introduction 50 years ago. The third, *Lasius fuliginosus*, has large, long-lived colonies (with thousands of workers) that collect honeydew from aphids, and in many ways the species appears to play the ecological role of the red wood ant group that is abundant in the conifer forests of northern Europe (Dobrzanska 1966; Quinet & Pasteels 1991). To examine species differences in the possible function of antennal contact, we compare the extent to which each species changes the frequency of contact in response to food.

Next we consider the possibility that ants might use antennal contact to assess density. For example, if contacts among a given number of nestmates tend to occur at regular intervals, a change of ant density may cause a change in the frequency of contact. There is much evidence to suggest that social insects may respond to changes in the numbers of other workers present, both nestmates and non-nestmates. This ability could facilitate predator avoidance (Munger 1984; Nonacs 1990); the allocation of workers to various tasks, including foraging (Gordon 1986, 1987; Seeley 1989;

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Robinson 1991); and the appraisal of enemy strength in territorial disputes (Hölldobler 1981; Adams 1990). How workers might assess density, that is, numbers of ants per unit area, is not known. No individual is capable of counting total numbers of workers; some simpler local cue would be required.

As a first step in investigating whether the rate of antennal contact may provide ants with a cue to nestmate density, we ask, how does contact rate change as density changes? Here we will use 'contact rate' to mean the number of contacts per ant, per unit time; the measures used in each experiment will be described below. Recent theoretical work shows how the average rate of contact within a group or colony of ants will depend on the movements of each individual, and on the tendency to move towards nearby ants (Adler & Gordon 1992). Ants have species-specific movement patterns, both in the shape of paths and the speed of movement (Harkness & Marouda 1985; Leonard & Herbers 1986). If individuals tend to move in similar ways, then for given densities and substrate conditions, the frequency of contact should be fairly regular.

Models of the relation of contact rate and density have been derived to describe contact rates of one predator with a collection of moving prey (Holling 1966). To apply these to contact rates of a number of moving objects with each other, it is necessary to assume that a contact does not alter the subsequent paths of the participating individuals (Okubo 1980). Observations of ants suggest this condition is not met. However, one feature of an appropriate null model for ant contact rates is as follows. If contact were a consequence of purely random collisions, contact rates would follow the laws of Brownian motion (for a basic discussion, see Feynman et al. 1963): in a system of N particles, the number of pair-wise collisions one particle experiences, per unit time, is proportional to N. The collision rate of two particles is proportional to $2N$, and so on; the total pair-wise collision rate of N particles is proportional to N^2. This null model predicts how numbers of contacts should depend on numbers of ants, if contact arises from random collisions.

Here we consider whether contact rate in *L. fuliginosus* is the result of random collisions, or whether instead ants behave in some way to regulate contact rates as density changes. To do this, we observed ants at different densities. In laboratory experiments, we placed different numbers of ants in arenas of varying size, in undisturbed conditions. The results led us to investigate the factors influencing the ants' distribution in the arenas, and whether an ant can perceive another at a distance.

We then examine the response of *L. fuliginosus* to changes of density in unusual conditions, by introducing non-nestmates. We consider whether ants respond to the proportion or number of non-nestmates present, and the role of contact rate in this process.

METHODS

All experiments involved observations of ants in an arena with a grid underneath it. We counted numbers of brief antennal contacts and numbers of ants in each square of the grid, for a specified length of time. A contact was considered to occur between two ants if both ants touched antennae, or if two ants within head-to-head contact range of each other slowed down, causing a visible kink in the path of each, and a visible head movement occurred. A contact lasts several hundredths of a second, so the duration of contact is negligible relative to the duration of observations (1–3 min). (If one ant touched its antennae to the abdomen of an ant in front of it, this was not counted, for two reasons: such contacts were relatively rare and because they were not symmetric, their inclusion would have entailed more complicated calculations of density effects.) Two measures of contact rate were derived. 'Overall contact rate' is defined as total number of contacts, summed over all regions observed, divided by the total numbers of ants placed by us in the arena. 'Local contact rate' is the number of contacts in one region divided by the number of ants in that region.

Species Differences in Contact Rate at Constant Density

To investigate species differences in contact rate, three species were observed. The study was performed in the laboratory to permit observation of all contacts and to eliminate the effects of spatial heterogeneity; it would be interesting to study such effects in more natural conditions in future studies. There were three replicate colonies for each species. Each *M. rubra* colony contained a queen, no brood, and about 50–100 workers. Each *S. invicta* colony contained a queen, a small amount of brood, and about 500 workers. Each *L. fuliginosus* 'colony' consisted of about 150 workers, taken a week before observations began from a large queenless laboratory colony. All colonies were kept in plastic arenas (12 × 23 cm), which were coated on the sides with Fluon so that the ants could not climb out. Each colony had been in its arena for at least a week before experiments began. A grid under each arena divided it into four regions of equal size (6 × 11·5 cm). Of the four, one region contained food; another contained test-tubes partly filled with water and plugged with cotton that served as a nest; the remaining two regions were empty. The four regions were designated as (1) food, (2) nest, (3) next to food and (4) next to nest. Each experiment lasted for 9 days and included 8 days of observation (day 7 was omitted). Food, consisting of sugar solution and mealworms, or artificial diet for *S. invicta* (Banks et al. 1981), was provided on alternate days (days 2, 4, 6 and 9), immediately before the first observation. Observations were made three times a day, between 0930 and 1100, 1400 and 1515, and 1600 and 1730 hours.

In each observation, each of the four regions was observed for 3 min, during which we counted the numbers of ants present in the region after 30 s, and the total number of antennal contacts between ants in the region. For each observation, we calculated the ratio of the number of contacts in 3 min to the number of ants at 30 s. These local contact rates were used in an ANOVA examining the effect of presence of food (yes or no), day ($N=8$ days), days within food ($N=4$ days), colony ($N=$ three colonies), location ($N=$ four regions), time of day ($N=$ three periods) and the food × location, time of day × location, and food × time of day interactions. Results reported as significant for *M. rubra* met the criterion of a sequential Bonferroni test (Rice 1989) for significance at the 0·05 level; for *S. invicta* and *L. fuliginosus*, at the 0·01 level. An overall analysis using all three species was not performed because the large differences among species in mean contact rate would be expected to cause differences of variance.

Contact Rate and Changes of Density of Nestmates in *L. fuliginosus*

This and all experiments described below involved one ant species, *L. fuliginosus*. We observed groups of workers, that is, parts of colonies, in laboratory conditions; further work is needed to test whether similar behaviour patterns occur in intact colonies and in the field.

Changes of nestmate density

To determine how contact rate depends on density, both numbers of ants and arena size were varied. The experiment was repeated with three groups of ants, consisting of 100, 200 or 450 workers. Each group of ants was housed in a series of four arenas of increasing size (size 1: 25 × 25 cm; size 2: 50 × 50 cm; size 3: 75 × 75 cm; and size 4: 1 × 1 m). The arenas were square, built of Plexiglas, with vertical sides that were coated with Fluon to prevent the ants from climbing out. For each arena size, and each size group of ants, the ants were kept in the arena for 3 days, during which six observations were made, twice a day. Therefore, for each group size, there were 12 days of observation (3 days per arena size, four arena sizes), and thus, the entire experiment for all three group sizes included 36 days of observation. After the first 12 days with 100 ants were completed, the 100 ants were returned to the larger colony from which they had been taken. Then 200 ants were chosen at random for the next part of the experiment; a similar procedure was used to obtain the 450 ants. Each new group of ants was left in the experimental arena overnight before observations began. Food, consisting of sugar water, was replenished daily before the first observation.

Under each arena, we placed a grid marked in squares of uniform size (6·25 × 6·25 cm). The numbers of grid squares for the four arena sizes were 16, 64, 144 and 256. In each arena, food was placed one grid square in from one corner, and water-filled test-tubes, to serve as a nest, were placed one grid square in from the diagonally opposite corner. On each day of observation, a series of counts was made twice, once between 0915 and 1130 hours, and once between 1400 and 1600 hours. Each session, or series of counts, consisted of a 3-min count of every grid square in the arena. For each count of a grid square, we recorded the total number of contacts in the square in 3 min, and, as a measure of the number of ants in the square, we recorded the maximum number of ants ever observed simultaneously inside the square in the course of the 3 min. In every session, we counted grid squares in the same sequence. At low densities, in the size 4 arenas, many grid squares were empty and more than one square was observed simultaneously. Antennal contact was counted as described above. It was not counted among ants on the food, or between ants in the course of trophallaxis. At very high densities (e.g. 450 ants in the size 1 arena), numbers of contacts were sometimes so high that it was impossible to be sure that all contacts were counted. A cut-off point of 150 contacts/3 min was chosen; values of 150 or more contacts in 3 min were recorded as 150.

Attraction to edges versus maintaining contact rates: an edgeless arena

In experiments in arenas of increasing size, ants tended to go to the edge of the arena as density decreased, and contact rates were higher at the arena edges. This suggested two hypotheses. First, ants are attracted to edges, and the resulting higher local contact rate at the edges is merely an irrelevant consequence of this. Alternatively, ants go to the edge in order to achieve a high local density there as arena size increases, thus maintaining contact rates at some threshold. To distinguish these two possibilities, ants were placed on a sphere, that is, an edgeless arena. Two spheres were used, corresponding in surface area to the two smallest arenas, sizes 1 and 2. The surface area of the smaller sphere (size 1) was 590 cm^2; that of the larger was 1964 cm^2 (those of arenas sizes 1 and 2 were 625 and 2500 cm^2, respectively). To cover the surface of the sphere with a grid of regions of equal size, 20 triangles of equal size were arranged as on the surface of an icosahedron (Cundy & Rollett 1961). On the larger sphere (size 2), each triangle was bisected, to give 40 grid triangles each of area 49 cm^2; on the smaller sphere, there were 20 grid triangles each of area 29·5 cm^2.

The spheres were plastic toy balls, which were first coated with white paint and then covered with the triangular grid described above. Each sphere was then covered with a tightly stretched nylon stocking to create a surface to which it was easier for the ants to hang on, and suspended from above by a stick glued to the north pole of each sphere. A Fluon-covered baffle was placed on the stick a few inches above its juncture with the sphere so that ants that did climb up would fall back onto the sphere. Three small water-filled test-tubes were glued onto the equator as a source of water, and cotton soaked in sugar water was attached to the equator on the other side as a source of food. Foragers of *L. fuliginosus* often travel on large tree branches to reach aphids, so the ants, captured when foraging, may have been familiar with surfaces with curvature similar to that of the spheres.

Two hundred ants were placed on each sphere. Even on the smaller sphere, ants were not sufficiently crowded that they had to disperse to avoid overlap (note that surface areas were as shown in Fig. 3, sizes 1 and 2). Ants did not hold on to each other. Ants that had fallen off the sphere were replaced before each count. Food was replenished each day before the first observation. Observations were conducted as in the arenas, twice a day, between 0930 and 1030 hours and between 1400 and 1500 hours. Ants were observed for 3 days (both spheres on the same days), for a total of 120 counts for the smaller sphere (20 grid triangles, two counts per day for 3 days) and 240 counts for the larger sphere (40 grid triangles). Each observation included a 3-min count, for each triangle in the grid, of the numbers of contacts, and maximum number of ants ever observed in that triangle during the course of the 3 min.

In analysing the data, two measures of aggregation were used. First, we used Pielou's (1977) index of dispersion, based on the ratio of the variance to the mean distribution of numbers of ants, to test whether distributions were significantly non-random. Results reported as significant met the criterion of a sequential Bonferroni test (Rice 1989) for significance at the 0·01 level. Second, to determine whether aggregation was more pronounced as overall density was decreased by moving the same number of ants to the larger sphere, we used Fisher's distribution for the analysis of clustering on a sphere (Pearson & Hartley 1972). Fisher developed this test to determine whether the earth is in the centre of the galaxy by asking whether the stars as viewed from the earth appear to be clustered. We tested whether, viewed from the centre of the sphere, the ants were clustered. Each count of the numbers of ants in each triangle on the icosahedron grid was assigned a direction from the centre of the sphere to the centroid of the grid triangle. For the larger sphere, data for the two halves of each bisected triangle were combined, giving 20 triangles of larger size. For each observation, including counts of all grid triangles, R is the resultant mean vector of ants' directions over all grid triangles, close to 0 for a random distribution and approaching 1 when all points are clustered at a point on the sphere. Significance tests were performed for R, based on Rayleigh's test for randomness. K, based on

Fisher's distribution, measures the extent of concentration around a given point on the sphere, corresponding to a given direction from the centre of the sphere. A cross-section through Fisher's distribution at the preferred direction looks like a normal distribution with standard deviation $1/K$. K is related to R as $\cot(K) - 1/K = R$.

Tendency to aggregate, and scanning distance, in a flat arena

The ants' preference for the edge of an arena, and their tendency to cluster on the sphere, are both forms of aggregation. To regulate contact rate, ants must be able to perceive each other before they come into contact, and decide in advance whether to turn towards each other. Aggregations will form when moving animals tend to turn toward each other (Turchin 1989). We measured tendency to aggregate, and scanning distance, in *L. fuliginosus*. Two hundred ants were placed in the size 2 (50 × 50 cm) arena. A grid was placed under the arena. The area of each grid square (1·2 × 1·2 cm), was our estimate of the scanning distance of an ant, or the distance within which one ant can perceive another through olfactory or visual cues; 1·2 cm is about twice the length of a worker. The ants were filmed on videotape. In analysing the film, sequences were chosen in which an ant seemed to be going in a straight line. To qualify as the focal ant, it had to walk through three successive, vertically aligned grid squares. In each of three cases, 50 ants were observed: (1) an ant was present in the grid square alongside the focal ant, or in the square diagonally above the focal ant; (2) an ant was present one grid square away, either in the square next to the one alongside the focal ant, or the square above that; and (3) no ants were nearby, that is, no ants were present in the two adjacent rows in the two adjacent columns. The focal ant was counted as either continuing in a straight line, turning towards the nearby ant, or turning away from it. In the third case, the focal ant was counted as either continuing in a straight line, turning right or turning left.

Response to Encounters with Non-nestmates

Contact rate in response to encounters with non-nestmates

Experiments described above examined how in undisturbed conditions, alterations of nestmate density affect contact rate. Here, to investigate response to altered nestmate density in disturbed conditions, we examined the effect of introducing non-nestmates. Ants were added to host groups of two sizes, 35 and 75 ants. In all experiments, 15 ants were added. To vary the colony identity of ants being encountered, added ants were either from the same colony, colony A, or another colony, colony B. Colony B was located several miles from colony A, and it is unlikely that ants from the two colonies had ever met before. Four experiments were performed: 35A + 15A, 75A + 15A, 35A + 15B, and 75A + 15B. Thus, the experiment measures responses to different numbers of encounters between host and added ants, and compares the effect of adding nestmates and non-nestmates.

In each experiment, the host ants were placed in a container (24 × 12 cm) and allowed to settle for at least half an hour before the experiment began. All added ants were marked the previous day with a spot of white paint. The container was placed on a grid of 18 larger squares (4 × 4 cm) used in counts of contact rate, within which were smaller squares (1 × 1 cm) used in measurements (described below) of individual speed. All experiments were recorded on a videotape of the entire container. The host group was undisturbed for 24 min. At the beginning of minute 25, the 15 ants were added and filming was continued for a total of 50 min. Each of the four experiments was performed twice. Contact rate and speed were measured from the videotape films. In each of the 18 grid squares, we counted the numbers of contacts in 1 min (not 3 min as in experiments described above). All grid squares were counted simultaneously by replaying the videotape, and the use of film meant that measurement error could be greatly reduced. For each experiment, contacts and numbers of ants in each square were counted at 15, 20 and 23 min, before ants were added, and at 25, 26, 27, 30 and 35 min, after ants were added (see Fig. 7).

In the data analysis, we used overall contact rate: total number of contacts occurring simultaneously in all 18 grid squares, divided by the total number of ants in the container at the time. The data analysis used differences between time periods in mean overall contact rates: the overall contact rate in one experiment averaged over the counts for 15, 20 and 23 min (time 1: before ants were added), the counts for 25, 26, and 27 min (time 2: immediately after ants were added), or minutes 30 and 35 (time 3: 5 min after ants were added). To measure the effect of adding ants, we compared contact rates before and immediately after ants were added (time 2 –

time 1). To determine how long changes in contact rate continued, we compared contact rates 5 min after and immediately after ants were added (time 3 – time 2). To determine whether introducing ants caused a lasting change in contact rate, we compared contact rates 5 min after ants were added with contact rates before ants were added (time 3 – time 1). For each comparison, there were eight differences (four experiments, two replicates). Each set of eight differences was used in a separate two-way ANOVA in which we considered the effect of mean difference (whether the difference was different from zero), main effects of number of host ants (75 or 35) and identity of the added ants (colony A or B), and the interactions of host number and identity of added ants. Results reported as significant met the criterion of a sequential Bonferroni test (Rice 1989) for significance at the 0·05 level.

Speed of movement in response to encounters with non-nestmates

Increases in contact rate might result from increases in the speed of the ants' movement. Speeds were measured from the same videotapes of the experiments described in the previous section by counting the numbers of smaller grid squares (1 × 1 cm) an ant entered in 10 s. In each minute that speeds were counted, we measured the speeds of the 12 host ants and 12 marked ants that we added. It was obvious that ants at the edges tended to cover less ground than ants in the middle. The arenas used in these experiments were plastic boxes that curved where the sides met the bottom (unlike the four arenas of increasing size described above), and some ants spent a lot of time trying unsuccessfully to run up the curved side of the container. To avoid a bias due to ants slowing down at the edges, each of the 12 ants measured consisted of six ants chosen from ants that were at the edge when the count began, and six from ants in the middle. Here the edge was defined as within 1 cm of the side of the container; the middle was defined as at least 4 cm from the edge.

To test for differences in speed between added and host ants, we considered the data for minute 25 only, immediately after ants were added. An ANOVA was performed using all counts obtained in minute 25 (speeds of 12 host ants and 12 added ants) in the eight experiments, a total of 196 counts. Effects tested were number of host ants (35 or 75), colony identity of added ants (colony A or B), and identity of the ants measured (host or added), as well as the number of host ants × host versus added interaction, and the colony identity of added ants × host versus added interaction. Results reported as significant met the criterion of a sequential Bonferri test (Rice 1989) for significance at the 0·05 level.

RESULTS

Species Differences in Contact Rate at Constant Density

The three species differed in local contact rate, i.e. numbers of contacts in a region divided by numbers of ants in the same region. Local contact rates appeared to be much higher in *L. fuliginosus* than in *M. rubra* or *S. invicta* (Fig. 1). This may be an effect of worker size; since a *L. fuliginosus* worker is two to three times as long as a small *S. invicta* worker, and about twice as long as a *M. rubra* worker, the same number of *L. fuliginosus* workers in an area of a given size may collide more often. However, if body size alone caused this difference, *M. rubra*, which is larger than *S. invicta*, should have shown higher contact rates.

The three species differed in the extent to which contact rate responded to changes of environment (Table I). For example, in *S. invicta*, contact rate was more differentiated than in *M. rubra*. Contact rate in *S. invicta* varied significantly with time of day (Table I: line d) and depended on the interactions between the presence of food and time of day (line g) and between the presence of food and location in the arena (line h). In *M. rubra*, only the effects of location (line e) and colony (line f) were significant.

In *S. invicta*, and to a lesser extent in *M. rubra*, there was an effect of food on the location of high contact rates (Fig. 2; Table I: line h). In *M. rubra*, contact increased around the nest when food was present (Fig. 2a), though this effect was only barely significant ($P = 0·05$; Table I: line h). Workers encountering food appeared to return to the nest tubes and engage in contact with ants there. This often preceded the formation of a trail of ants to the food, suggesting that in *M. rubra*, brief antennal contact may be involved in recruitment. In *S. invicta*, contact rate increased near the food when food was present (Fig. 2c); foragers may be recruited from ants nearby instead of from ants

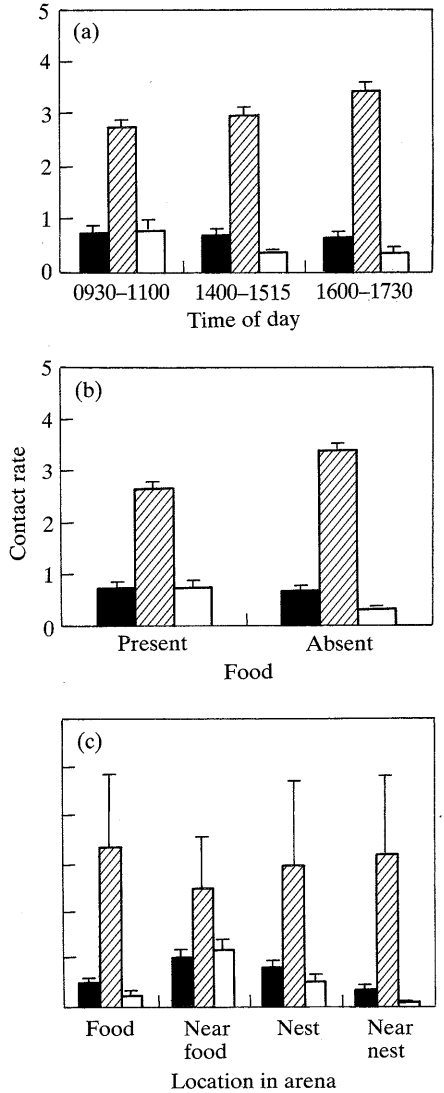

Figure 1. Mean (+SE) species differences in contact rate. (a) Contact rates at three times of day; (b) contact rate on days when food was present or absent; and (c) contact rate in the four regions of the arena. Shown is a measure of local contact rate, the mean ratio of number of contacts to number of ants in each region, in the course of 3-min observations. ■: *M. rubra*; ▨: *L. fuliginosus*; □: *S. invicta* Buren.

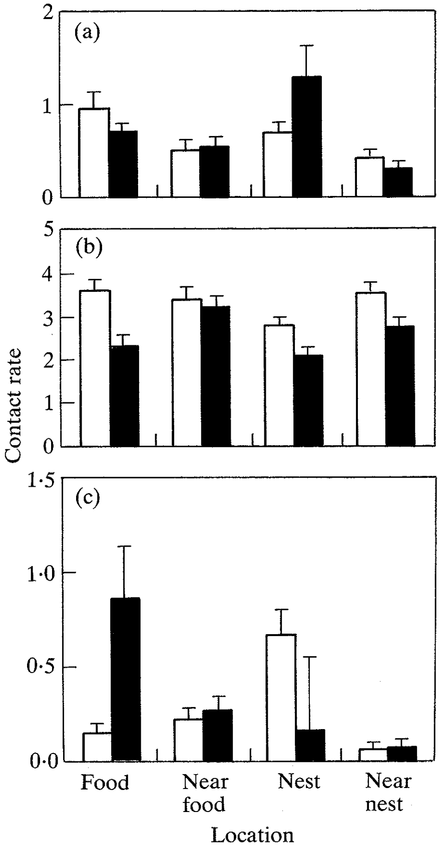

Figure 2. Mean (+SE) species differences of contact rate: interaction of food and location. (a) *M. rubra*; (b) *L. fuliginosus*; (c) *S. invicta* Buren. Contact rate is the mean ratio of number of contacts to number of ants in each of four regions, in the course of 3-min observations on days when no food was present (□) and when food was present (■).

back at the nest. In *L. fuliginosus* there was no significant food × location interaction (Fig. 2b). In this species, contact rates were consistently, although not significantly, higher in all locations when food was not present.

Contact Rate and Changes of Nestmate Density in *L. fuliginosus*

Attraction to edges versus maintaining contact rates; an edgeless arena

Changes of density had one obvious effect on the distribution of ants in the arenas: as density decreased, ants were more likely to go to the arena edge, and contact was more likely to occur at the edge. For example, the results of 200 ants in the four arena sizes are shown in Fig. 3. In larger arenas, as density decreased, higher numbers of ants and numbers of contacts were found at the arena edges. The numbers of ants (Fig. 4a) and numbers of contacts (Fig. 4b) at arena edges both

Table I. Results of ANOVAs examining contact rate (number of contacts observed in 3 min divided by number of ants) in three species*

		M. rubra			*L. fuliginosus*			*S. invicta*		
Effect	*df*	*SS*	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*
(a) Food (present or not)	1	0·3	0·3	NS	38·9	27·0	0·001	14·1	36·2	0·001
(b) Days within food	6	9·0	1·8	NS	154·2	1·5	NS	22·9	3·8	NS
(c) Day (8)	7	9·3	1·6	NS	193·1	19·2	0·001	37·0	13·6	0·001
(d) Time of day (3)	2	0·2	0·1	NS	30·1	10·5	0·001	12·7	16·3	0·001
(e) Location (4)	3	17·8	7·1	0·001	30·2	6·9	0·001	49·1	16·4	0·001
(f) Colony (3)	2	27·5	16·5	0·001	2·8	1·4	NS	12·5	15·9	0·001
(g) Food × time of day	2	0·7	0·4	NS	5·4	2·3	NS	20·1	25·8	0·001
(h) Food × location	3	7·9	3·1	0·05	10·3	2·4	NS	12·9	11·0	0·001
(i) Time of day × location	6	9·8	1·9	NS	5·0	0·6	NS	17·7	7·6	0·001
Error	261	218·1			377·3			101·5		

*Means and standard errors are shown in Figs 1 and 2.

increased in larger arenas. To derive the measures shown in Fig. 4, all six observations for each group and arena size were pooled. Each proportion shown is the ratio of the total numbers (ants or contacts) observed in the grid squares at the edge of the arena, divided by the total numbers (of ants or contacts) in all grid squares. But as arena size increased, the proportion of grid squares at the edge decreased. To correct for this, each proportion was weighted by dividing it by the expected proportion at the edge, that is, the proportion of edge squares in that size arena. (Proportions of edge squares, out of edge plus middle squares, were 0·78, 0·45, 0·30 and 0·23 for arenas of size 1, 2, 3 and 4, respectively).

In the four arenas of increasing size, the area increased quadratically, in proportions 1, 4, 9 and 16, but the edge increased only linearly, in proportions 1, 2, 3 and 4. Thus by staying at the edge, the ants kept local densities high as arena size increased. We tested the response of ants to an edgeless arena, a sphere. If the tendency to go to the edge results simply from an attraction to the edge, then on a sphere, in the absence of an edge, ants should be distributed uniformly. However, if the tendency to go to the arena edges is a means of maintaining density, then ants should aggregate even in the absence of an edge, the more so as density decreases.

Ants tended to aggregate on the spheres (Table II). Data from each observation were considered separately because the location of the most dense aggregation of ants changed from one observation to the next. In general, ants tended to aggregate near a point corresponding roughly to the south pole of the sphere, apparently preferring to be upside down. Counts of numbers of ants in each grid triangle showed a significant tendency to aggregate in two of the six observations on the smaller sphere (Pielou's index, Table II). On the larger sphere, there was a significant tendency to aggregate in all six observations. R is 0 when points are randomly distributed and R is 1 when the points are most clustered. Significance tests for R led to conclusions identical to those from Pielou's test (Table II).

Aggregation increased as density decreased. K, Fisher's measure of the extent of aggregation on a sphere, increases when clustering increases. All values of K on the larger sphere were higher than any on the smaller sphere (Table II).

On an edgeless arena, ants aggregated more when densities were low. This suggests that in the flat arenas, ants move to the edges at low densities in order to keep density high, not because of an unrelated preference for edges.

Tendency to aggregate and scanning distance

Ants that changed direction were likely to turn towards an ant in an adjacent square (Table III). The crucial value was the 15 turns made by focal ants towards ants in the adjacent square. If the direction of the turn were random, the expected number of turns would be seven, the mean number of turns over all three cases, shown in the two columns on the right in Table III. The observed

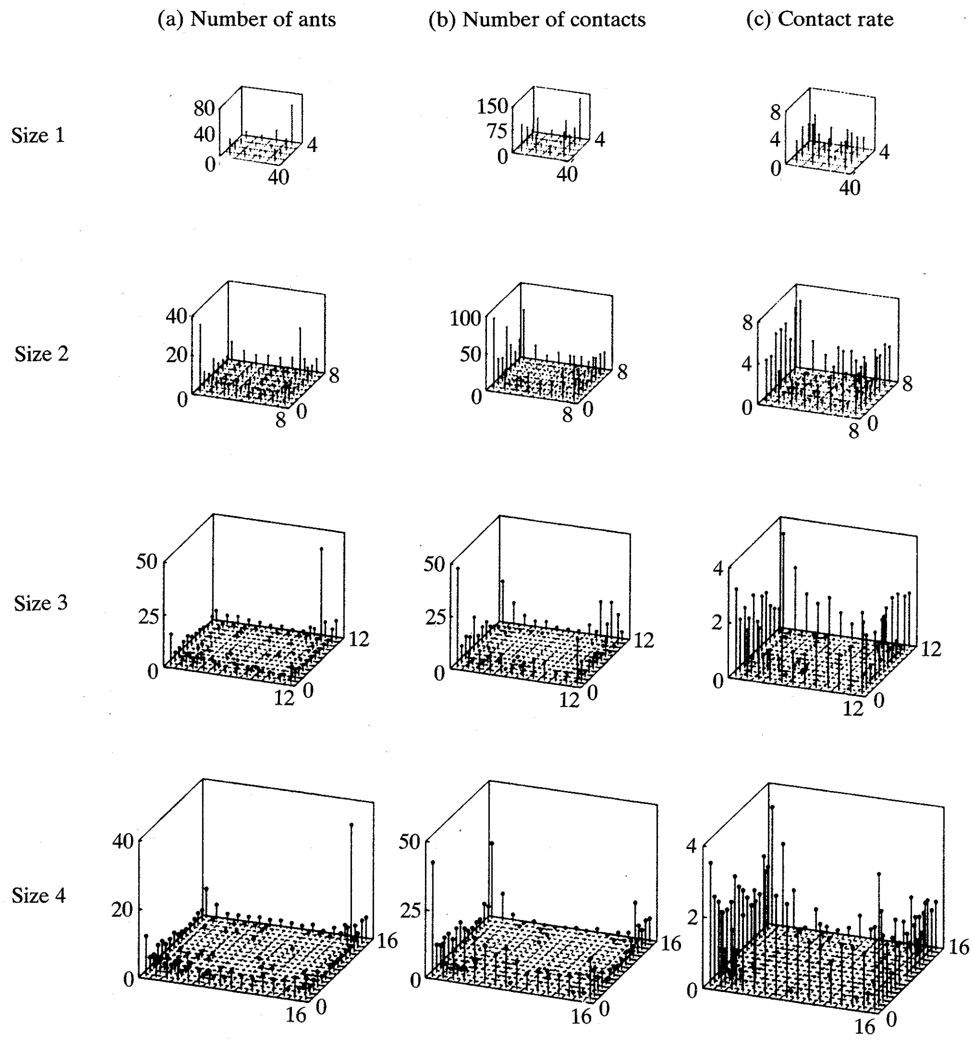

Figure 3. Distribution of ants and of contacts in arenas of increasing size. The abscissa shows: (a) mean numbers of ants; (b) mean numbers of contacts; and (c) mean contact rate. Contact rate is the ratio of numbers of contacts to numbers of ants in each grid square. The four arenas, shown vertically in order of increasing size, have areas of magnitudes 1, 4, 9 and 16. Grid squares were of equal size in all arenas.

value of 15 was significantly higher than seven (corrected value for chi-squared for that cell of the table is 8·04, $df = 1$, $P < 0{\cdot}01$).

It appears that 1·2 cm is a good estimate of the distance at which one *L. fuliginosus* worker responds to another. There was no apparent difference between an ant's tendency to turn towards an ant more than one grid square away and its behaviour when no ants were nearby. This indicates that ants more than one grid square away were unlikely to be perceived.

Ants can perceive each other at a distance, and make a decision whether to contact an ant 1·2 cm away. This means that ants can regulate contact rate by deciding in advance whether to turn towards another ant.

Overall contact rate as a function of nestmate density

To determine whether contact rate is regulated, we ask whether contact rate as a function of density

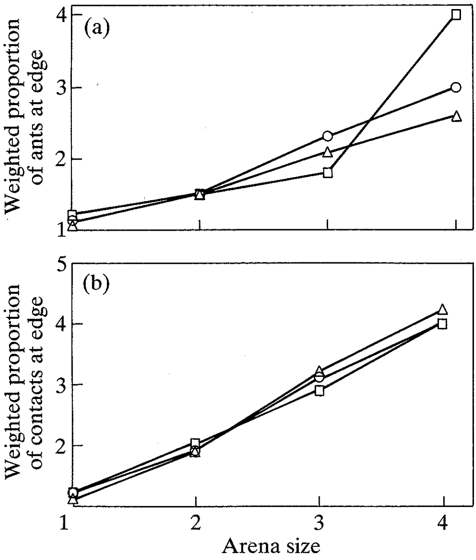

Figure 4. Ants at edges as density decreases. (a) Proportion of ants at the edge of the arena, weighted by expected proportion, in four arenas increasing in size from 1 to 4. (b) Proportion of brief antennal contacts occurring at the edge of the arena, weighted by the expected proportion, in four arenas increasing in size from 1 to 4. ○: 100 ants; △: 200 ants; □: 450 ants.

behaves as it would if it were random. According to the principles of Brownian motion, in an area of a given size, the collision rate experienced by each one of N randomly moving particles is proportional to N. Figure 5 shows contact rate as a function of density. Here, to summarize the data as simply as possible, we use overall contact rate: the total number of contacts observed, divided by the total number of ants in the arena. This effectively weights contact rate by the number of ants in each square, reducing the influence of empty grid squares (Pacala 1988). Counts of contacts for all grid squares were summed for all six observations of each arena and group size. Density was calculated as the total number of ants in the arena, divided by the area of the arena, where arena sizes 1–4 were considered to have areas of 1, 4, 9 and 16 (e.g. the density of 100 ants in arena size 4 was 6·25 (100/16)).

Overall contact rate did not increase linearly with numbers of ants (Fig. 5). Instead, as numbers of ants per unit area, or density increased, overall contact rate levelled off. Thus, the results show that the ants do not behave like particles in Brownian motion; contact rates were not the consequence of random collisions. The number of contacts each ant experienced did not increase with the number of ants (Fig. 5). Overall contact rate did appear to increase linearly with density when densities were very low. But at higher densities, contact rate levelled off. For example, in Fig. 5, the square symbol at density near 50 and an overall contact rate near 25, represents the overall contact rate for 450 ants in the size 3 arena. The triangle at a density of about 200 and an overall contact rate near 22, represents the overall contact rate for 200 ants in the size 1 arena. Here the ratio of densities, or number of ants per unit area, is about four to one, but the overall contact rates were approximately the same.

Local contact rate as a function of nestmate density

A simple null model of numbers of contacts per unit time in a given area, or local contact rate, would be: $C = a\,Nq$, where C is number of contacts, a is a constant and N is the number of ants present. It follows that $\ln C = \ln a + q \ln N$. The slope, q, of $\ln C$ as a function of $\ln N$, is the rate at which total numbers of contacts increase as a function of the number of ants present. If contact is completely random, occurring as it would for particles in Brownian motion, q should be equal to 2 (Feynman et al. 1963).

Keeping in mind that in the absence of a detailed null model, data analysis can only be exploratory, the slope of the number of contacts as a function of the (maximum) number of ants in the same grid square was calculated for each group size, using a linear regression (Table IV). For each size of arena and group of ants, data from all six observations were pooled. Some counts were 0, and all data (x) were transformed to $\ln(x+1)$. Edges and middles of each arena were considered separately. The total numbers of points used in each regression depended on the numbers of grid squares counted for each arena size, from 16 squares for size 1 arenas to 256 squares for size 4 arenas. For example, in the size 1 arena, the regression for edges involved 66 points (11 edge squares, six counts each). Counts for the two squares containing the food and the nest, both in the middle of the arena, were not included. Degrees of freedom for regression for edges were 65, 167, 262 and 359 for arena sizes 1, 2, 3 and 4; for middles they were 17, 203, 588 and 1163 respectively.

Table II. Tendency to aggregate on a sphere, showing, for each of six observations, the value for Pielou's index of dispersion, degrees of freedom and significance values for the corresponding test for non-random distributions, and *R* and *K*, measures of the extent of clustering from Fisher's test. (See text for details)

Observation	Index of dispersion	*df*	*P*	*R*	*K*
Small sphere					
1	90·59	17	0·001	0·336	1·083
2	64·59		0·001	0·294	0·933
3	30·87		NS	0·119	0·362
4	10·65		NS	0·107	0·323
5	20·77		NS	0·177	0·543
6	16·0		NS	0·164	0·498
Large sphere					
1	148·06	37	0·001	0·608	2·458
2	149·81		0·001	0·473	1·660
3	121·77		0·001	0·554	2·102
4	132·26		0·001	0·570	2·198
5	97·84		0·001	0·547	2·056
6	143·95		0·001	0·496	1·775

Table III. Tendency to turn towards a nearby ant, showing number of times an ant changed direction in response to the presence of another ant ($N = 50$ ants for each case)

	Behaviour		
Case	Continue straight	Towards other	Away from other
Ant in adjacent grid square	30	15	5
Ant one grid square away	40	5	5
No ant within two squares	38	5 (right)	7 (left)

As density increased, local contact rate did not (Table IV, Fig. 6). Figure 6 shows the regression coefficients, or slopes, listed in Table IV, and plotted as a function of density. Local contact rates are clearly less than 2, showing that contact rate did not behave according to a simple null model of random behaviour. All regression coefficients were significant ($P < 0·001$) except for those for 450 ants, size 1, edge and middle ($P > 0·05$) (Table IV).

Local contact rate appears to decrease at high densities, as a result of the low values for 450 ants, size 1 (Fig. 6). At this density, and only at the edges, it was frequently necessary to stop at the cut-off point of 150 contacts in 3 min. We calculated how large the error in the measured value of 150 contacts would have to be to achieve a regression coefficient near 1, and thus eliminate the apparent decrease in local contact rates. Using the data from arena edges for 450 ants, size 1, four artificial data sets were created, in which any numbers of contacts at the cut-off point of 150 contacts were converted to 175, 300, 500 and 1000, respectively, while other values for contact rate, and all observed values for numbers of ants, were retained. Regressions of contact rate on numbers of ants were performed as above, and showed that to obtain a coefficient near 1, the true numbers of contacts measured as 150 would often have to exceed 500 (giving a coefficient

Table IV. Local contact rates in arenas of increasing size, showing the slope, or regression coefficient, the standard error, and R^2 resulting from the regression of ln (number of contacts) on ln (number of ants) in each size of arena (1–4) and each group size of ants (100, 200, 450)

	Edge			Middle		
Arena size	Slope (q)	SE slope	R^2	Slope (q)	SE slope	R^2
100 ants						
1	1·66	0·16	0·79	2·21	0·32	0·75
2	1·57	0·09	0·66	0·48	0·05	0·33
3	1·55	0·07	0·67	0·19	0·02	0·17
4	1·03	0·05	0·55	0·16	0·01	0·17
200 ants						
1	1·34	0·11	0·71	1·81	0·35	0·63
2	1·82	0·12	0·59	0·58	0·09	0·63
3	1·62	0·07	0·65	0·37	0·02	0·28
4	1·86	0·07	0·69	0·21	0·02	0·15
450 ants						
1	0·16*	0·08	0·06	0·29*	0·56	0·02
2	0·45	0·03	0·51	1·35	0·08	0·56
3	1·86	0·09	0·65	1·44	0·06	0·51
4	1·68	0·08	0·56	0·88	0·03	0·46

*Indicates only those regression coefficients that were not significant ($P<0·001$).

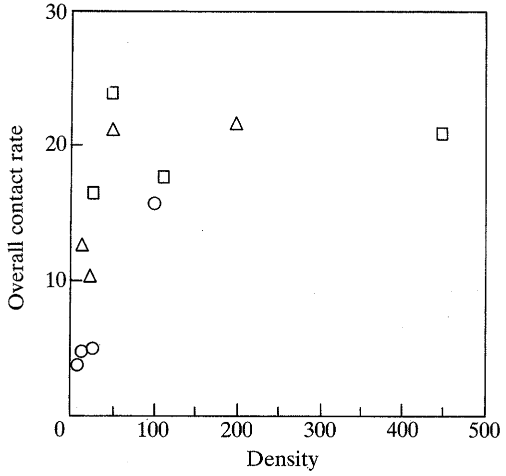

Figure 5. Overall contact rate as a function of density. Contact rate is the sum of all contacts in the arena, divided by the total number of ants in the arena. Density is the total number of ants divided by the area of the arena. For a given number of ants, larger arenas entail lower densities, shown to the left; smaller arenas, of higher densities, are shown to the right. ○: 100 ants; △: 200 ants; □: 450 ants.

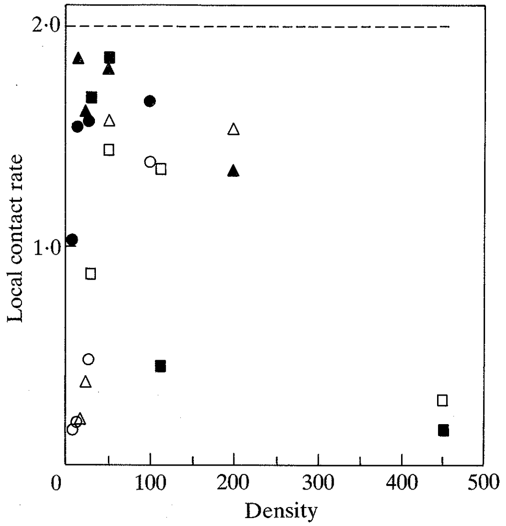

Figure 6. Local contact rate as a function of density. Contact rate is the regression coefficient of the number of contacts as a function of number of ants in the same grid square (6·25 × 6·25 cm); see Table IV. ○: 100 ants; △: 200 ants; □: 450 ants. Filled symbols represent contact rates at the edge of the arena; open symbols represent contact rate in the middle of the arena. Data were transformed by ln (x + 1). The dotted line shows a slope of 2, predicted by a null model.

of 0·67). However, the cut-off point of 150 contacts was never reached before the 3-min count was almost over, indicating true numbers were never as high as 500. Thus, it appears that the decrease in contact rates for 450 ants in the arena size 1, does reflect a true decrease in local contact rate at high density, though the magnitude of the decrease remains uncertain.

Local contact rate, like overall contact rate, was regulated, not random.

Comparing overall and local contact rates

Ants appear to regulate contact rate by curtailing contacts with nearby ants when densities are high. For example, compare the results for 200 ants, size 1, in Figs 5 and 6. At this density, overall contact rate had already begun to level off (Fig. 5). But this was not the case for the local contact rate at this density (Fig. 6). How did 200 ants decrease overall contact rate at this density when the local contact rate at the same density was still high? The answer may be that 200 ants, even in the smallest arena, could still avoid contact, and decrease overall contact rates, by moving into a relatively empty square (Fig. 3a, size 1). When 450 ants were crowded into the smallest arena, however, there was no possibility of spreading out. Instead, the means of reducing contact rate had to be active avoidance of contact with ants in the same grid square. This may be reflected in the reduced local contact rates for 450 ants in Fig. 6.

Ants tended to preserve overall contact rate as density changed, but both overall and local contact rates varied with numbers of ants and location in the arena. First, numbers of ants affected overall contact rate independently of arena size. For a given density, overall contact rate tended to be higher in larger groups of ants. At densities up to about 50, overall contact rates at a given density were generally higher for 450 ants than for 200, which were higher than for 100 (Fig. 5). Second, local contact rate varied with location in the arena, tending to be higher at the edges than the middle of the arena. In Fig. 6, local contact rates for arena edges tend to be clustered above those for arena middles. Ants at the edge contacted each other more often than did similar numbers of ants in the middle.

On the spheres, there was little evidence that ants regulated contact rate, either overall or local, at the higher density. Overall contact rate on the smaller, size 1 sphere (density 201) was 50·11, an extremely high value compared with those in arenas at the same density (about 22; see Fig. 5), while overall contact rate on the larger, size 2 sphere (density 60·6) was 33·25 also somewhat high. The local contact rates on the spheres were not much higher than in the arenas: 1·45 for the smaller sphere, and 2·59 for the larger one. It may be more difficult to decrease contact rate on a sphere than on a flat arena. In a flat arena, when ants aggregate along the edge, contact is suppressed on one side by the wall, and on the other by the paucity of ants at the long edge of the line-shaped cluster. On a sphere, however, aggregations tend to be round, so more ants are in the centre of the cluster.

While ants regulate contact rate as density changes, contact rate clearly depends to some extent on numbers of ants and on the shape of the surface.

Contact Rate in Response to Encounters with Non-nestmates

When ants encountered non-nestmates, contact rates increased. In general, overall contact rate increased significantly whenever ants were added (Table V; effect of overall mean difference, $F_{1,4}=343{\cdot}8$, $P=0{\cdot}001$), and decreased again after 5–10 min (see times 2 and 3, Fig. 7). Contact rates increased more when non-nestmates were added (effect of identity of added ants, $F_{1,4}=32{\cdot}2$, $P=0{\cdot}005$).

It appears that the response of host ants depends on their rate of contact with added ants. Everything else being equal, each of the 35 host ants would encounter one of the 15 added ants more often than would each of the 75 host ants. Increases in contact rates were significantly higher when ants were added to groups of 35 host ants than when they were added to groups of 75 host ants (effect of number of host ants, $F_{1,4}=13{\cdot}8$, $P=0{\cdot}021$). The effect of host number was especially pronounced when non-nestmates were added (interaction of host number and identity of added ants, $F_{1,4}=16{\cdot}1$, $P=0{\cdot}016$). Although overall contact rates were somewhat higher in groups of 75 host ants than in groups of 35 host ants (Fig. 7), possibly reflecting a two-fold increase in density, the smaller groups showed a greater increase in response to added ants.

It was not possible to determine the extent to which host and added ants each contributed to the increases in contact rates, in response to added ants, because the mark on the added ants was sometimes not visible on film. Added ants appeared to circulate among the hosts; there was no visible

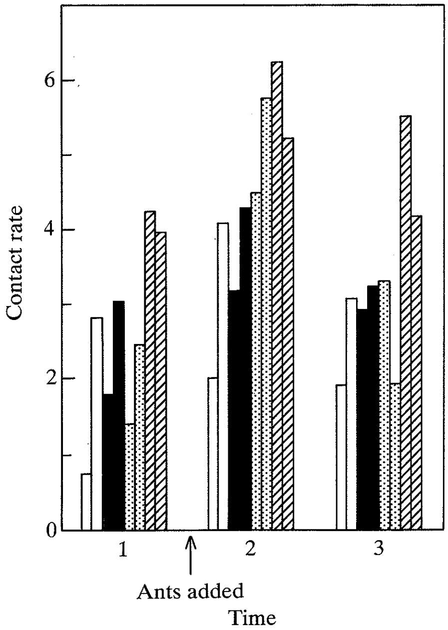

Figure 7. Contact rate in response to encounters with added ants. Each bar shows the mean contact rate for one colony. Two replicates are shown for each experiment. Time 1 shows the mean for minutes 15, 20 and 23, before ants were added; time 2 shows the mean for minutes 25, 26 and 27, immediately after ants were added; time 3 shows the mean for minutes 30 and 35, 5–10 min after ants were added. □: 35 host ants, nestmates added (A + A); ■: 75 host ants, nestmates added (A + A); ⊡: 35 host ants, non-nestmates added (A + B); ▨: 75 host ants, non-nestmates added (A + B).

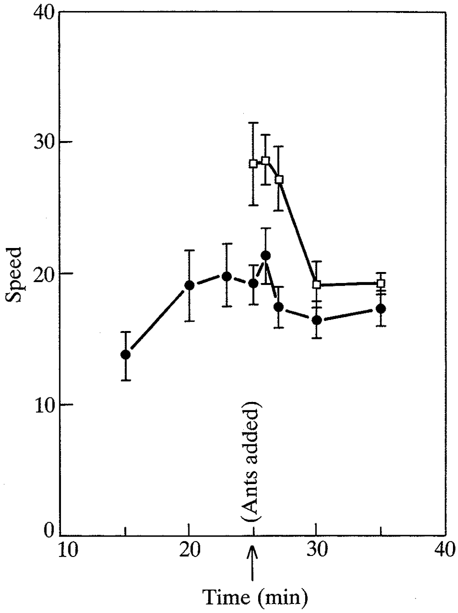

Figure 8. Mean (±SE) speed in response to encounters with added ants. The figures show the results for one replicate of one treatment, 75 host ants of colony A with 15 of colony B added. ●: Speeds of host ants; ○: speeds of added ants. Speed is measured as the number of grid squares, 1 × 1 cm, entered by an ant in 10 s. Each point represents the mean speed of 12 individuals. Ants were added immediately before observation began at minute 25.

tendency for added ants usually to contact other added ants.

The increase in contact rate, although highly significant, was short-lived. Contact rates 5 min after the introduction of other ants, nestmates or not, were no different from those before introduction (no significant effects for ANOVA comparing time 3 and time 1). In all four treatments, contact rates 5–10 min after ants were added were significantly lower than those up to 3 min afterwards (mean difference in contact rate = −1·15; ANOVA for effect of mean difference, $F_{1,4} = 10{\cdot}1$, $P = 0{\cdot}05$; no other effects were significant).

Speed of movement in response to encounters with non-nestmates

The results on the speeds at which host and added ants moved did not account for the concurrent increases in contact rate. To provide an example of the results, Fig. 8 shows the data for one of the eight experiments, one of the two trials in which 15 non-nestmates were added to a group of 75 host ants. Speed varied considerably from one minute to the next, even in undisturbed groups of ants before any further ants were added.

Overall contact rates, of both host and added ants, increased most when 15 non-nestmates were added to 35 ants (Table V). But the highest speeds were those of the 15 non-nestmates added to the group of 75 host ants. All ants, both host and added, moved significantly faster when there were 75 host ants than when there were 35 host ants (Table VI; mean speed for experiments with 75 host ants, 23·3 ± 1·1 1-cm grid squares entered in 10 s; for experiments with 35 host ants 18·5 ± 0·9, $N = 96$ for both). Since the highest contact rates did not occur when speeds were highest, it appears that increased contact rate is not simply a consequence of increased speed.

Table V. Increase in contact rate immediately after 15 ants from the same colony (nestmates) or another colony (non-nestmates) were added to a group of 35 or 75 host ants

Number of host ants	Colony identity		
	Nestmates	Non-nestmates	Mean of both
35	1·25	3·17	2·21
75	1·31	1·64	1·48
			Overall 1·84

Contact rate is calculated as the number of contacts in 1 min divided by the total number of ants present in the arena. Each number is the difference in contact rate, averaged over the 3 min after ants were added, from the contact rate averaged over 10 min before ants were added (time 2 − time 1).

Table VI. Speed of movement immediately after ants were added, based on results of ANOVA using speed, as number of grid squares traversed in 10 s, in the minute that 15 ants, either from the same colony (nestmates) or another colony (non-nestmates) were added to a host group of 35 or 75 ants

Effect	*df*	SS	*F*	*P*
Host number	1	1135·9	13·06	0·0004
Colony identity of added ants	1	812·6	9·35	0·003
Added versus host ants	1	837·5	9·63	0·002
Host number × added versus host ants	1	1·9	0·02	0·88 (NS)*
Colony identity × added versus host ants	1	584·5	6·72	0·010
Error	186	16172·8		

*NS at $P > 0{\cdot}01$, sequential Bonferroni test.

All ants moved significantly faster when non-nestmates were added than when nestmates were added (mean speed for non-nestmates 22·9 ± 0·9, for nestmates 18·8 ± 1·1; $N = 96$ for both). Added ants moved significantly faster than host ants (mean speed for added ants 22·9 ± 1·1; for host ants 18·8 ± 0·9; $N = 96$ for both). There was no significant interaction of host number and host versus added ants. The interaction of the colony identity of added ants with host versus added ants was caused by higher speeds of the added non-nestmates (26·8 ± 1·4) than the added nestmates (19·2 ± 1·4), while speeds for host ants were similar in both cases (host ants when nestmates were added, 18·5 ± 1·4; host ants when non-nestmates were added, 19·1 ± 1·4). ANOVA results are shown in Table VI.

This experiment involved four different expected rates of contact between hosts and added ants (for hosts, encounters of 35 or 75 hosts with 15 added; for added ants, encounters of 15 added with 35 or 75 hosts). Of these four cases, the highest expected numbers of encounters would be for the 15 added to the group of 75 host ants. This group, the 15 added to 75, showed the highest speed, especially when the 15 added ants were non-nestmates (Fig. 8). This indicates that when an ant experiences many contacts with non-nestmates, it moves faster, possibly because it becomes alarmed. However, the highest contact rates were in the group of 15 non-nestmates added to 35 host ants. Thus high speeds do not account for high contact rates. It appears that besides moving faster, an ant that encounters many non-nestmates also acts in some other way that further increases its rate of contact with all other ants.

DISCUSSION

The studies reported here were conducted in laboratory conditions; further observations in the field are needed. Nevertheless, several lines of evidence suggest that patterns of antennal contact are an important feature of the social organization of ant colonies.

First, there are species-specific differences in patterns of antennal contact, and these are consistent with other, ecological differences among species. *Solenopsis invicta* is a colonizing species that reacts quickly to move into disturbed environments. Local contact rate in *S. invicta* is extremely sensitive to the presence of food (Figs 1 and 2). This corroborates previous results that the rate of antennal contact among *S. invicta* ants exploring a new region increases if food is present (Gordon 1988). In addition, contact rate in *S. invicta* is spatially and temporally patterned (Figs 1 and 2). *Lasius fuliginosus*, by contrast, has very long-lived colonies that use a stable resource, aphid populations in deciduous forests. In this species, local contact rate is relatively stable (Figs 1 and 2). In the laboratory experiments presented here, there were differences in colony size and composition as well as differences among species. For example, groups of *L. fuliginosus* workers were kept in arenas without a queen or brood. This probably affected hunger levels and other aspects of forager behaviour. However, in repeated observations many groups of workers showed similar and predictable behaviour patterns, suggesting the behaviour observed is a species-specific characteristic. Field studies are needed to confirm this.

The second line of evidence indicating the importance of contact rate is that ants regulate the frequency of contact in undisturbed conditions, keeping contact rates relatively constant as density changes (Figs 5 and 6). Contact rate is not a simple consequence of random collisions among ants; instead, the rate of contact is modified by the ants' behaviour. This suggests that the rate of contact has some function in the organization of ant colonies. At low densities, ants aggregate, which helps keep overall contact rates up. In a flat arena, they aggregate along the edge of the arena (Fig. 4). In the absence of an edge, when ants were placed on a sphere, they still aggregated, and did so more at lower densities (Table II). Observations from videotape records show that individuals can decide in advance whether to move towards another ant and engage in contact, because an ant can perceive another at a distance of 1·2 cm (Table III).

At high densities, both overall and local contact rates were lower than would be expected if contact were random (Figs 5 and 6). When densities are so high that ants cannot avoid contact by moving away from nestmates, they appear to curtail the number of contacts with the ants nearby. Contact rate also may level off at high densities through changes in the speed or spatial configuration of ants' movements. While the results presented here show that *L. fuliginosus* workers regulate contact rate, there remains much to be learned about how they do so. This will require analysis (at a range of densities) of speeds, path shapes and ants' moment-to-moment decisions whether seek or avoid contact.

The third line of evidence indicating the importance of contact rate comes from experiments in which ants were exposed to ants of another colony. Ants responded to the proportion, not number of non-nestmates encountered. This demonstrates that ants can use the rate at which they encounter other ants as a cue. When ants of another colony were present, contact rates increased (Table V). When higher proportions (not numbers) of non-nestmates were present, contact rate increased significantly more.

Contact rate increased dramatically, about three-fold, immediately after the addition of non-nestmates (Fig. 7), while similar increases in the density of nestmates in undisturbed colonies led to much smaller changes of contact rate (Fig. 5). To compare the results of the two experiments, note that in the added ants experiments, the arena was roughly half the size (288 cm^2) of the size 1 arena (625 cm^2). Thus when 15 ants were added, density increased from 70 to 100 as numbers of ants increased from 35 to 50 (e.g. density of 70 represents 35 ants divided by an area of 0·5), and density increased from 150 to 180 when numbers of ants increased from 75 to 90. In undisturbed colonies, similar increases of density (70 to 100, 150 to 180) produced only a slight increase in contact rate (Fig. 5).

One way for ants encountering non-nestmates to increase contact rate would be for individuals to move faster. However, the results presented here show this is not the only relevant mechanism. In addition, it appears that individuals increase contact rates by altering their decisions about how many contacts to engage in with nearby ants. Detailed analysis of ants' paths is needed to determine when and how, in response to disturbance, an ant changes its tendency to contact another.

Why should ants regulate contact rate in undisturbed conditions? The results show that contact rate does not fluctuate as much with changes in numbers of ants as it would if it resulted from random collisions. If ants transmit information when they touch antennae, keeping the frequency of contact relatively constant may stabilize decision-making behaviour at the colony level. Recent theoretical work supports this suggestion (Adler & Gordon 1992; Gordon et al. 1992), but more empirical work is needed. One possibility is that contact rate is involved in short-term adjustments in worker allocation. An ant colony generally engages in a variety of tasks. The numbers active in each task vary from hour to hour, subject to changes in the current requirements of the colony. The numbers of ants engaged in one task depend on the numbers engaged in another (Gordon 1987, 1989). For example, if a harvester ant colony increases the numbers of workers actively engaged in nest maintenance, then a distinct group of individuals, the foragers, become less active. If workers can distinguish contacts with nest maintenance workers from contacts with foragers, a large change in the interval between successive contacts with nest maintenance workers may alter a forager's behaviour. In honey bees, *Apis mellifera*, the behaviour of foragers is influenced by the time interval between arrival at the hive and contact with a nectar storer (Seeley 1989). Such cues may be used by ants as well. Regulating the rate of contact in undisturbed conditions may facilitate an individual's ability to recognize when a shift in worker allocation leads to a change in the interval between contacts. This conjecture will require further investigation, in intact colonies and in a variety of conditions.

Why should ants increase contact rate when non-nestmates are present? In conflicts between neighbouring colonies, workers of some ant species respond to changes in the relative density of nestmates and non-nestmates (Hölldobler 1981; Adams 1990). An ant that suddenly encounters alien ants may be in danger; either it has left its own colony's territory, or an invasion has occurred. The proportion of its contacts that are encounters with non-nestmates is a measure of the extent of the danger. By increasing the rate of contact with all other ants, the ant may be able to assess the situation more quickly, because from a more rapid sequence of contacts it will gain information sooner about the numbers of non-nestmates present. The increase in contact rate, though short-lived, may be sufficient to generate a defensive response to intruders.

Further investigation of contact rate, and its place in the diverse ecology of ants, may shed some new light on the organization of social insect colonies. Contact rate is an appealing candidate as means of assessing nestmate density, because it requires only simple behaviour from each individual ant. In the course of antennal contact, an ant can recognize another as a nestmate. Ants might perceive contact rate as a frequency, i.e. numbers of contacts per unit time, or they might perceive the time interval between contacts, which would be a consequence of contact rate. Investigation of sensory mechanisms would be needed to distinguish these, but the following account is plausible. An ant may have a threshold for time intervals between contacts with nestmates. If this threshold is met, the status quo is maintained, and no alteration in behaviour occurs. If the interval between contacts is too long, the ant becomes more likely to decide from a distance to turn towards another ant. If the interval is much too short, it avoids contact with nearby ants. If contact with non-nestmates is too frequent, it seeks contact with nearby ants. These simple rules could produce a pattern that reliably informs the ants of changes of density in unusual conditions, such as an influx of non-nestmates. Well-regulated networks of brief antennal contact have evolved in ants. To understand how ant colonies are organized, we will need to consider how these networks function.

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