

The expandable network of ant exploration

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Abstract. The Argentine ant, *Linepithema humile*, adjusts its exploratory behaviour according to group size. Colonies of three different sizes were allowed to explore novel, empty arenas of three different sizes. Ants were tracked on videotape using a computerized image analysis system. At high densities, the shape of searchers' paths becomes more convoluted; at low densities, paths are more linear. Previous theoretical work shows that this relation between individual path shape and group size maximizes the discovery rate of the group as a whole. Temporal patterns were examined in density of ants in the novel arena, path shape, and the rate at which area covered by the group expanded. The density of ants in the novel arena increased over the course of 40 min of exploration, but there were no significant temporal patterns of path shape. The area covered by exploring ants increased more rapidly early in the exploration (after 5 min in the novel arena) than later on (after 20 min). The results show that individual ants adjust the shape of their paths in a way that maximizes the discovery rate of the group as a whole. This provides an intriguing new example of how individuals, each acting independently, can generate group-level behaviour.

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Social insects provide compelling examples of collective behaviour. Individuals, each using only local information, work together to perform effectively as a group. Social insects, like many vertebrates, forage in groups. Foraging behaviour varies with group size in vertebrates (e.g. Caraco 1979, 1980; Giraldeau 1988; Packer et al. 1990; Lott 1991), and with colony size in social insects (e.g. Gordon 1991, 1992). We know little, however, about what decisions individual foragers make to alter their behaviour in response to group size, and whether these decisions contribute to the foraging success of the group as a whole.

How foragers move will determine the probability of finding food (Bell 1991; Benhamou 1994). For ants, movement patterns determine the probability of finding anything. Ants have very poor vision and rely mostly on chemical cues; to perceive an event, an ant must come close to it or to the cloud of odour it emits. Thus ants move around, not only to search for food, but also to monitor all aspects of their environment. When an ant encounters a noteworthy event, such as a food source, intrusion or disturbance, it can communicate its discovery to its nestmates. The paths of

moving ants create a network that covers a region. As the number or density of searchers varies, the network of paths may have to expand or shrink to cover space effectively. In this study I examined whether ants adjust the shape of their paths as group size varies, to increase the likelihood that if something important occurs, some ant will find it.

Searching Behaviour in Individuals and Groups

Are individual ants capable of adjusting their path shapes to maximize discovery rates for the group of searching ants as a whole? Detailed studies of the movements of individual ant foragers show that ants searching for food move differently from ants retrieving food (e.g. Wehner et al. 1983). Recent studies showed that foraging ants adjust searching behaviour in response to the distribution and durability of food sources (Leonard & Herbers 1986; Fourcassie et al. 1992; Traniello & Kozol 1992; Fourcassie & Traniello 1993, 1994). Here I asked whether ants adjust path shape in the short term (<1 h) in response to the numbers of other ants participating in a bout of exploration.

From the pioneering work of Berg (1953) to more recent studies of foraging and exploratory

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behaviour (e.g. Jander 1975; Pyke 1978; Kareiva & Shigesada 1983; Bovet & Benhamou 1988), most work on movement patterns deals with individual foragers. Theoretical work makes a variety of predictions for how the shape of a forager's path affects the rate at which a forager may discover new events, such as food sources. For example, Pyke (1978) found that in an infinitely large region, the optimal search path is a straight line. Zimmerman (1979) showed that a random walk is optimal when food is distributed in patches so abundant that none can be depleted in one visit. Stillman & Sutherland (1990) showed that the same is true if patches regenerate quickly. Finally, Bovet (1981) found that a path shape between a random walk and straight line is preferable for central-place foragers. All of these findings apply only to individual foragers.

In a group of foragers, the relation of an individual's searching behaviour to the effectiveness of its group's search is complex (Cody 1971; Harkness & Maroudas 1985; Warburton & Lazarus 1991). As with solitary foragers, path shape and food distribution will be important, but the effects of those factors will further depend on interactions among individuals. Until recently, most work on movement patterns in groups was theoretical because empirical studies were almost impossible. Paths of group members had to be traced from film by hand (e.g. Okubo et al. 1977; Gordon 1988) because computerized systems were unable to track multiple paths. Recently there has been great progress in the use of image analysis to study searching behaviour in many animals, including ants (e.g. Fourcassie & Traniello, in press). The innovation introduced here is the capacity to track the paths of hundreds of individuals simultaneously.

Modelling Path Shape

Adler & Gordon (1992) examined how the discovery rate of a group of individual searchers depends on path shape and number of searchers. In their model, searchers moved around a space in which events appeared at random locations. Discovery rate was measured as the proportion of events discovered by all individuals. Path shape was characterized using a measure of turning angle (e.g. Kareiva & Shigesada 1983). Suppose an animal moves from point A to point B, and again from B to C; each transition is defined as a

'step'. The turning angle is the angle between the two steps: the angle between the line connecting A and B, and the line connecting B and C. Standard deviation of turning angle, measured over all the steps of an animal's path, characterizes the tortuosity or linearity of the path. The turning angles of a tortuous path, such as a random walk, have a very high standard deviation; those of a path that traces a straight line or a perfect circle, in which every step is at the same angle relative to the previous step, would have a standard deviation of 0.

In the following, 'turning index' will be used to mean 'standard deviation of turning angle'. High values of the turning index indicate a high propensity to turn; low values indicate a more linear path. This measure of path shape is derived directly from the diffusion theory introduced to biology by Berg (1953). Subsequent authors have used other measures that emphasize the amount of ground covered (e.g. Bell 1985; Johnson et al. 1992; Fourcassie & Traniello 1994); these measures of displacement are derived from those of path shape (Kareiva & Shigesada 1983). Standard deviation of turning angle was used in Adler & Gordon (1992) because of its mathematical tractability; it is used in the empirical work presented here to provide a direct test of the model.

In Adler & Gordon's (1992) model, the path shape that maximizes the discovery rate of a group depends on the number of individuals that are searching (Fig. 1). A high turning index can lower the discovery rate: searchers travelling on very tortuous paths will search the same area over and over, and will fail to discover events located in the spaces between individuals. Because of this, when there are few searchers, a low turning index (i.e. a more linear path) leads to a higher discovery rate for the group as a whole. But the detrimental effects of a high turning index are reduced when the number of searchers is large. When searchers are crowded, any region is likely to be searched by some individual, even if no individual's path covers much ground, so most events are likely to be discovered. Thus, turning index has little effect on the discovery rate of the group as a whole when there are large numbers of searchers. The prediction of this model, then, is that at low density (number of individuals per unit area), turning index should be low, reflecting more linear paths; at higher density, turning index is less important and so may increase.

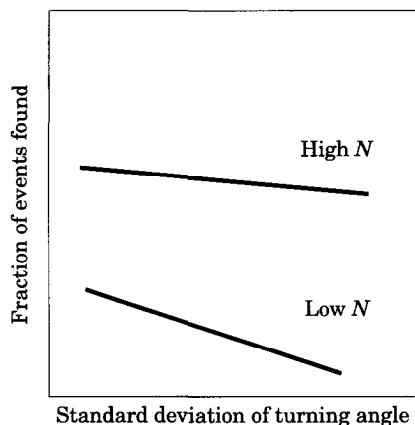


Figure 1. Theoretical prediction (Adler & Gordon 1992) for how discovery rate (fraction of randomly placed events discovered in a fixed time) and path shape (standard deviation of turning angle) depend on N , the number of searchers. At high N , high standard deviation of turning angle has little effect on fraction of events found, reducing it by only about 10%. At low N , high standard deviation of turning angle decreases the fraction of events found, reducing it by about 50%.

This study was conducted with the Argentine ant, *Linepithema humile* (= *Iridomyrmex humilis*). This species' worldwide success as an invader (Crowell 1968; Bond & Slingsby 1984) indicates proficiency at finding food. To test how the shape of the paths of exploring ants depends on worker density, I introduced colonies of different sizes to novel arenas of different sizes.

I examined whether there is a temporal pattern in the shape of ants' paths as exploration proceeds. Previous studies suggest that there is a temporal pattern of numbers of ants entering a novel region to explore it (Wilson 1962; Aron et al. 1989; Detrain et al. 1989; Deneubourg et al. 1990), and of the path shapes of exploring ants (Gordon 1988). If path shape is related to density, and there is a temporal pattern of density, then an analysis of path shape requires some understanding of the temporal pattern.

A group's capacity to spread out and expand the area it covers depends on the shape of searcher's paths. If path shape changed as the group's search proceeds, so would the rate of expansion of area covered. To test this directly, I measured rate of spread at different times since the onset of exploration.

Finally, I examined the relation between encounter rate and nestmate density during the

course of exploration. Previous work suggested that some ant species use encounter rate as a cue to nestmate density (Gordon et al. 1993). That work showed that the ant *Lasius fuliginosus* curtails encounter rate at high densities; here I consider whether *L. humile* does this as well.

METHODS

Experiment 1: Path Shape, Encounter Rate and Nestmate Density

Procedure

I performed experiments with nine colonies, each containing one to three queens and brood. Colonies were housed in plastic boxes (bottom surface 31×21 cm) with water-filled test-tubes, fitted with tight cotton plugs, as a nest for queens, brood and associated workers. All colonies were fed crickets and artificial diet (Bhatkar & Whitcomb 1970) on the same days, and always on the day before trials were performed. There were three colony sizes: Small (about 300 workers), Medium (about 500 workers) and Large (about 1000 workers). These were colony sizes, all with about the same amount of brood, when the experiment began; all colonies produced workers during the 6-week period of the study and increased somewhat in size. There were three replicate colonies of each size.

Each novel arena explored by the ants consisted of a glass ring, an 8-cm-high section of a cylinder, placed on a flat piece of glass. Because the edge of the ring was flat, ants could not escape beneath it. A ring of grease on the upper inside edge of the ring kept the ants from escaping over the top edge. I used three sizes of arena: Small (15 cm diameter), Medium (30 cm) and Large (45 cm).

I introduced each colony to every arena size, for a total of 27 trials (3 arena sizes \times 3 colony sizes \times 3 replicate colonies of each size). All experiments were performed from 1200 to 1700 hours, 3 days a week, with three different colonies tested each day in the order dictated by a Latin square design. At least a day elapsed between successive trials using the same colony. The 27 trials took 3 weeks.

Before each trial, the entire bottom surface of the arena was wiped with a piece of cotton dipped in sugar water, and then was wiped dry with a clean piece of cotton. This procedure created a

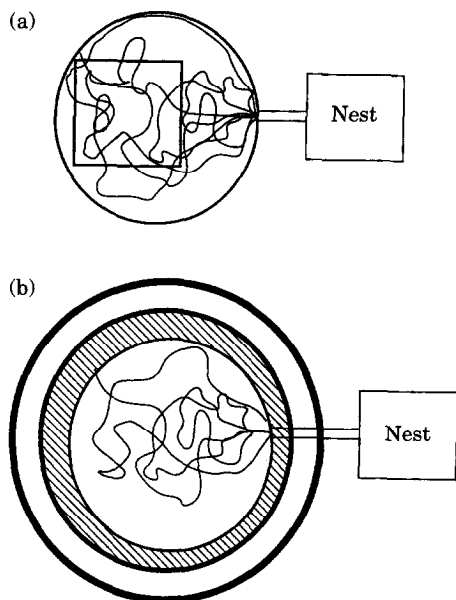


Figure 2. (a) Experimental set-up for exploration of novel arenas. Ants were kept in a plastic box (Nest) that was connected by Tygon tubing to a circular, empty arena. Ants were filmed as they explored the arena. Later, computer software was used to track the paths of the ants in a rectangular region of the videotape image. (b) Experimental set-up for measure of rate of spread by a group of exploring ants (see text).

faint residue of sugar which was attractive to the ants, although unlike the food the colonies usually received, but there was no discrete food source to discover or collect. The arena was placed on a Just-Normlicht light table to provide high contrast for videotaping. The light table generated some heat, but the glass of the arena bottom was 1.7 cm thick, providing some insulation, and ants did not appear to behave any differently when the light table was on or off. The nestbox was connected by Tygon tubing to the arena, via a hole in the side of the nestbox and another in the side of the glass ring (Fig. 2a). Ants were free to enter and leave the novel arena throughout the trial. The arena was videotaped from above using a Sony CCD-V101 video-camera fitted with a Tokina $\times 0.5$ wide angle lens. Videotapes were made for 3 min at a time, at 5, 10, 20 and 40 min during the trial. Time 0 was when the first five ants had entered the arena from the nestbox. After the last 3-min videotape beginning at 40 min, the ants were collected from the arena by an aspirator and

put back into the nextbox. A total of 108 videotapes were made (27 trials, 4 times videotaped per trial). Although ants often went around the boundary or edge of the arena, I never observed a foraging trail to form anywhere in the middle, or away from the boundary, of the arena. Instead, ants spread throughout the arena in all trials.

During the 3 min of videotaping, an observer counted the number of ants in the arena at 0, 60 and 120 s.

Image analysis and measurements from videotapes

I analysed the videotapes using an IBM PC, an Imaging Technology VP1100 Frame Grabber, Panasonic AG1960 computer-controlled VCR, and image analysis software written by Garr Updegraff of Data Crunch. I analysed 120 of the 180 s of videotape using the image at every sixth frame (0.2 s; speed of videotape was 30 frames/s). The image analysis tracked the paths of all ants in a region of the arena selected from the video image (about 10×10 cm). In the Small arena, this region was a square with all corners near the circular boundary of the arena; in the Medium and Large arenas, it was a rectangle opposite the hole from which ants entered (as in Fig. 2a). I chose this side for analysis to focus on ants that had already spent some time in the arena. Because I did not include paths of ants immediately approaching or leaving the glass side of the arena in the analysed region, data on path shape do not include paths of ants as they turned back from the boundary.

The image analysis system tracks the path of each ant, assigning each ant an identification (ID) number. Whenever an ant enters the analysed region, it is identified as a new ant. In data analysis, I eliminated paths of ants that were tracked for less than 2 s, thus eliminating ants that moved briefly in and out of the analysed region. Figure 3 shows some typical ants' paths.

The following four measures were calculated for each ant's path. (1) Turning angle of each step (after the second). A step is defined as the line traversed between the positions of an ant in successive views six frames apart. At a median walking speed, a step was about 2.5 mm long, slightly less than an ant's body length. (2) Mean turning angle averaged over all steps in the path of the ant. Angles were measured in degrees. Number of steps per path ranged from 10 to 513.

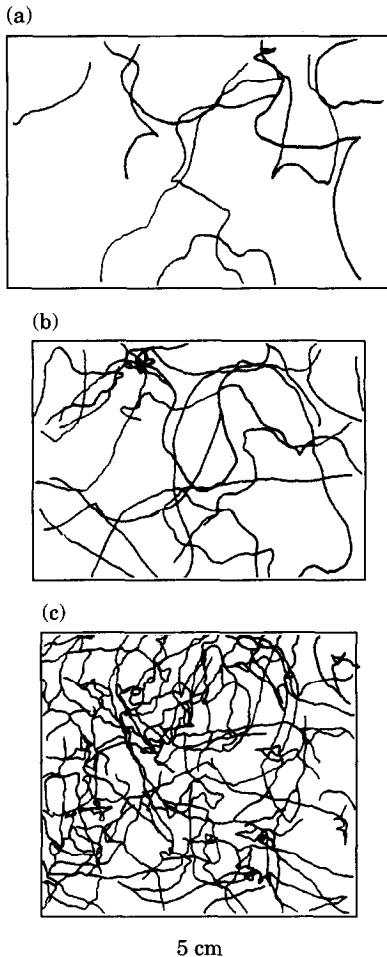


Figure 3. Illustration of some paths. Each figure shows the paths of exploring ants in a novel arena, traced by the image analysis of a region of the arena. The path almost enclosing the upper left corner of (a) consists of seven steps. Places where paths meet or cross represent an encounter only if the two ants were at the point of intersection at the same time; whether this occurred is not shown. (a) Low density (small colony, large arena) for about 70 s. (b) Medium density (medium colony, medium arena) for about 20 s. (c) High density (large colony, small arena) for about 10 s.

in most of the 108 trials, the longest paths tracked were between 100 and 200 steps (100 steps is 20 s). (3) Turning index (i.e. standard deviation of turning angle over the entire path of the ant). When angles are measured on π , $-\pi$, and periodicity is ignored (e.g. an angle of 90° is equivalent to an angle of -270°) then the maximum possible

standard deviation of turning angle, that of a random walk, would be $\pi/\sqrt{3}$ radians; the corresponding maximum in degrees is 103.9. (4) Time, location and ID for all ants involved, for each encounter between two or more ants. An encounter was identified by the image analysis program when two or more ants touched antennae, or when an ant touched the body of another with its antennae. The algorithm assigning ant IDs after encounters was based on the observation that ants of *L. humile* tend to proceed in the same direction after an encounter (personal observation). I checked the algorithm by running a graphics display of the ant paths, as tracked by the image analysis program, over the original videotape. A random assignment of ant IDs after pair-wise encounters would be correct 50% of the time; the procedure used here was correct about 90% of the time at lower densities (Medium and Large arenas).

The following measures were calculated for each 120-s videotape analysed. (1) Number of paths tracked. This is a measure of the number of ants ever to enter the 10×10 -cm analysed region during the 120 s; those present less than 2 s were eliminated, as described above. (2) Mean turning index, measured as mean of standard deviation of turning angle, averaged over all paths tracked. (3) Variation among ants (standard deviation) in turning index for all paths tracked. (4) Number of encounters between uniquely identified ant paths. Thus, if ants with paths labelled *a* and *b* met several times during the course of the videotape (which in fact rarely occurred) their encounters were counted as one. However, two paths identified as distinct ant IDs by the image analysis could have been made by the same ant that had left the analysed region and then re-entered it. (5) Area of the analysed region (approximately 10×10 cm, measured for each trial using a videotaped ruler).

Numbers of ant paths tracked ranged from three to 683 in the 108 videotapes. The total number of paths tracked was 19 083. Mean numbers of ants observed in the whole arena (averaged over three counts at 1, 2, and 3 min) ranged from 6.7 to 443.3.

Overall density is the mean number of ants in the whole arena, averaged over three counts made during the 180 s of videotape, divided by the area of the arena. I used this measure to assess the relation of density and path shape, because two observations suggest that density in the whole

Table 1. Correlation between turning index and density

	Symbol in Fig. 5	Density rank			r_s
		1	2	3	
Small colonies	\triangle	2	1	3	0.5
	\circ	1	3	2	0.5
	\square	1	2	3	1
Medium colonies	\triangle	1	2	3	1
	\circ	3	2	1	-0.5
	\square	1	2	3	1
Large colonies	\triangle	1	2	3	1
	\circ	1	3	2	0.5
	\square	1	3	2	0.5

Numbers shown are the ranks of the turning index, tabulated by ranked density. Each line shows the values for one colony; the shape is the one representing that colony in Fig. 5.

arena, not just in the analysed region, could affect path shape. First, ants passed in and out of the analysed region quite quickly; most ants were present for only 20–40 s out of the 120-s videotape. Second, ants appeared to circulate freely throughout the arenas.

To assess the relation between encounter rate and density, I calculated the local density of each analysed region, using the number of paths tracked by the image analysis divided by the exact area of the region (approximately 10×10 cm). This measure is appropriate because contact is only possible between ants that are very close together.

Data analysis

Temporal patterns in density and path shapes of exploring ants. To evaluate temporal patterns in path shape and density, I used curvilinear regression with the method of orthogonal polynomials (Sokal & Rohlf 1969). For path shape, measured as mean turning index (over all paths tracked in 120 s), and for overall density (numbers of ants counted in the whole arena divided by area of the arena), I estimated both the linear and quadratic trends. A positive linear trend denotes an increase of the variable with time, in this case either standard deviation of turning angle or overall density. A negative quadratic trend indicates a modification to the straight line, so that the curve is humped. A positive linear trend combined with a negative quadratic trend is consistent with a

curve that initially increases and then levels off. There were four sets of 27 polynomials (linear and quadratic sets each for overall density and mean turning index, 27 trials). To determine whether experimental conditions influence temporal trends in density or path shape, I used each set of 27 linear or quadratic polynomials in an ANOVA testing for an effect of colony size (3), arena size (3), and colony size \times arena size interaction.

Path shape and overall density. Colony size clearly had an important effect on density (Fig. 4a). Thus the relation of path shape and overall density in the whole arena is shown separately for the Small, Medium and Large colonies (Fig. 5). Because there was no significant temporal pattern of path shape, statistical analysis used the mean standard deviation of turning angle and overall density for each trial, averaged over all four times (5, 10, 20, 40 min). To avoid confounding the effects of variation between replicate colonies with the effects of density, I made statistical comparisons separately for each colony.

To test whether turning index is correlated with density, I found, for each colony, the Spearman's rank correlation coefficient (r_s) of mean standard deviation of turning angle and overall density (Table 1). This indicates whether turning index tended to increase as density did, in the three different trials with the same colony. I then found the average r_s for all nine colonies. Under the null hypothesis of no correlation, the mean $r_s=0$; on average, there would be no relation between

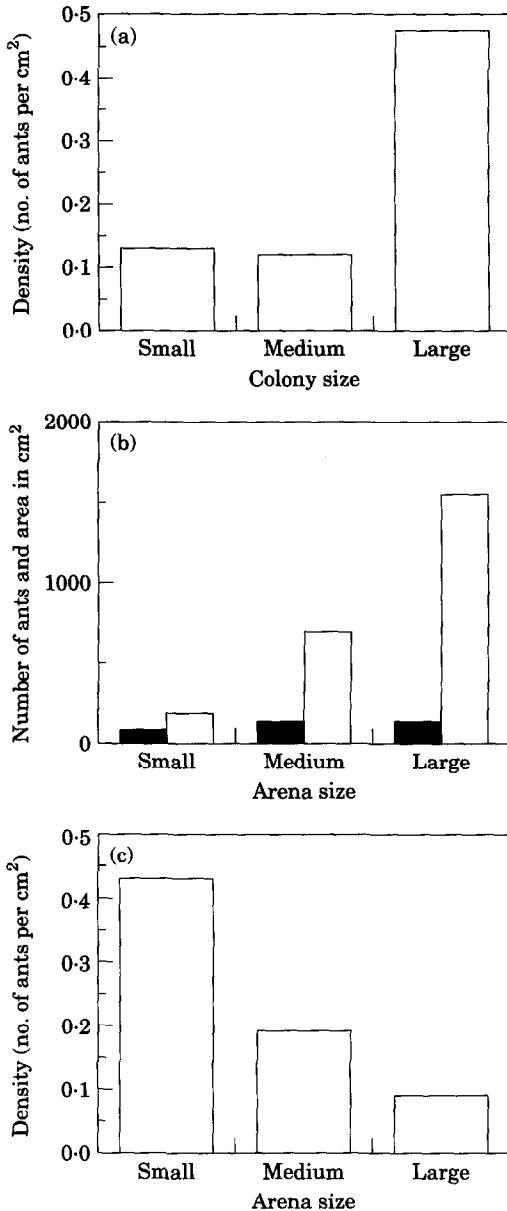


Figure 4. (a) Mean overall density (numbers of ants in the whole arena divided by area of the arena) as a function of colony size. (b) Mean numbers of ants (■) in the whole arena as a function of area of the arena (□). (c) Mean overall density of ants as a function of arena size.

turning index and density. I used the variance of the mean r_s to calculate z (corrected for continuity). Then to test whether the mean r_s differs

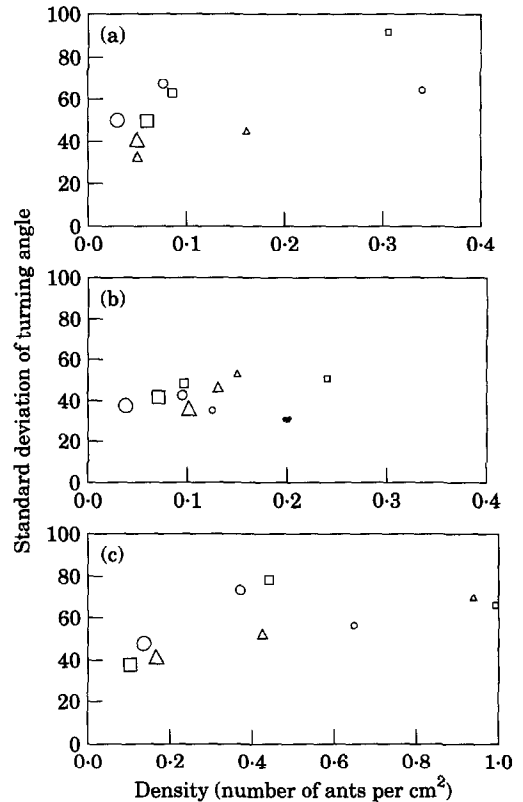


Figure 5. Turning index as a function of density in (a) Small, (b) Medium and (c) Large colonies. In each figure, symbols (○, □, △) represent three different colonies. For each colony, the size of the symbol is scaled to represent arena size (Small, Medium, Large). Each point shows the mean turning index (standard deviation of turning angle) for all ant paths (range 3–683 paths) tracked on one 120-s videotape, averaged over the four videotapes made at 5, 10, 20 and 40 min since the ants entered the novel arena. Mean overall density is also averaged over the four times.

significantly from 0, I compared z with critical values of the normal distribution.

Contact rate and local density. If contact rate were the result of random collisions, total numbers of contacts should be proportional to N^2 , where N is the number of ants. I plotted total numbers of contacts (measurement procedure described above) within the analysed region of the arena as a function of local density, number of ant-paths tracked within that region divided by its area. Encounter rate appears to be due to

random collisions; the results did not indicate otherwise. No further statistical analysis was attempted.

Experiment 2: Temporal Change in the Rate of Expansion

Procedure

I performed a separate experiment to compare how quickly ants expand the total area that they cover after 5 min and 20 min of exploration of a novel arena. I continued the same feeding schedule for all colonies as before, and set up experiments as before. The three glass rings, bounding arenas of three sizes, were placed concentrically (Fig. 2b). The nestbox was connected to the inner arena with Tygon tubing, as before: one piece of tubing led from the nestbox to the outer arena, a second led from the entrance hole of the outer arena to the entrance of the middle arena, and a third led to the inner arena. Thus, to travel from the nestbox to the inner arena, ants traversed a bridge (shown as lines in Fig. 2b), consisting of three contiguous pieces of tubing: from the nestbox to the outer, Large arena; from the Large to Medium arena, and from the Medium to the inner, Small arena. In the course of the experiment, the two inner glass rings were removed successively, and I measured the rate at which the ants spread into the newly accessible area.

There were two experimental conditions. In the first, ants were allowed into the small arena. After 5 min the Small arena's glass ring (bounding the arena) was removed, allowing the ants to spread into the Medium arena, so that they were then in an arena larger than, and containing, the region previously occupied. When the smallest glass ring was removed, so was its entrance tube, and at this point the tubing led from the nestbox to the hole in the Medium's arena's boundary glass ring. The Medium arena was videotaped for 3 min, beginning at the time the Small arena's boundary was removed. After 5 min in the Medium arena, the Medium arena's ring and tubing were removed, as before, allowing ants to spread into the Large arena's glass ring. The tubing now led only from the nestbox to the hole in the Large arena's glass ring. The Large arena was videotaped for 3 min, beginning at the time the Medium arena's glass ring was removed.

The second experimental condition followed the same procedure, but the ants were in each arena for 20 min before each ring was removed and ants were allowed to spread into the arena of the next size.

Both conditions were performed once with each of the same nine colonies used in experiment 1 (three colony sizes, three replicate colonies). As in experiment 1, at least 1 day elapsed between trials. The experiment lasted 3 weeks. From the videotapes, we counted the number of ants in the annulus between the Small and Medium arena edges at 1, 60 and 120 s after the Small arena's ring was removed, and the same in the annulus between the Medium and Large arena after the Medium arena's ring was removed. The first count, at about 1 s, began as soon as the ring had been fully removed from the videotape picture and was not blocking the observer's view of the ants.

Data analysis

To measure the rate at which ants spread from a smaller to larger arena, I found the difference between the number of ants in the annulus between the two arena boundaries at 60 and 1 s, and then the same difference at 120 and 60 s. For each colony size there were three replicate colonies. I found the mean difference, over the three replicates, for each colony size. For each of the three colony sizes tested for 5 min per arena before spreading and for each of the three colony sizes tested for 20 min per arena before spreading, there were thus two sets of differences, one measuring spread in the annulus between Small and Medium arenas, and the second measuring spread in the annulus between Medium and Large arenas. I then found the difference between corresponding rates of spread, for a given colony and arena size, in the 5-min and 20-min conditions (Table I). I tested whether each difference in the rate of spread after 5 and 20 min was statistically significant by finding its 95% confidence interval (Moses 1986).

RESULTS

Path Shape and Density

The overall density of ants (number of ants per cm^2) exploring the novel arenas depended on both

colony size and arena size. The number of ants exploring a novel arena increased with colony size, and was generally larger in the Large (1000 ants) colonies than in the Small (300 ants) or Medium (500 ants) colonies (Fig. 4a). The number of ants exploring the novel arena increased only slightly with arena size, whereas the area of the arenas increased quadratically over the three arena sizes (diameters 15, 30, 45 cm; Fig. 4b); as a result, density decreased with arena size (Fig. 4c). Densities were highest by far for Large colonies in Small arenas.

Temporal patterns in density

The overall density of ants in the novel arena increased over the course of the exploration (from 5 to 40 min after the ants entered the novel arena). For each of the nine combinations of colony and arena size, there were three replicate trials with different colonies. I found the median polynomial of the three replicates. For all nine colony/arena size combinations, the median linear polynomial for density was positive, indicating numbers in the arena increased over time.

Larger colonies increased numbers in the novel arena more rapidly than smaller ones. There was a significant effect of colony size on the linear polynomial for density (ANOVA: sum of squares (SS)=2.9, $F_{2,18}=5.8$, $P<0.01$) due to a stronger increase in density over time in larger colonies ($\bar{X} \pm \text{SE}$ linear polynomial for Small colonies = 0.2 ± 0.05 , Medium colonies = 0.3 ± 0.16 , Large colonies = 0.9 ± 0.25 , $N=9$ for all means). There was no significant effect of arena size and no significant interaction of colony size \times arena size.

The quadratic polynomials for temporal change in density were mostly negative (median values for the three replicates each in eight of nine colony \times arena size combinations). The combination of a positive linear trend and negative quadratic trend indicates that the number of ants in the novel arena tended to increase initially, then level off later in the 40-min observation period. There were no significant effects of colony size, arena size, or the colony size \times arena size interaction on the quadratic component of temporal change in number of ants.

Temporal patterns in path shape

There were no strong temporal patterns in the turning index. The median for linear polynomials

was negative for six of the nine colony size \times arena size combinations, indicating that in these six combinations, the turning index decreased over time in the novel arena. However, three polynomials were strongly positive. For the quadratic component of temporal change in path shape, the median polynomial for seven of the nine colony size \times arena size combinations was negative, indicating that a plot of the turning index, as a function of time, was usually a humped curve. However, two of the nine polynomials were strongly positive. There were no significant effects of colony size, arena size, or the colony size \times arena size interaction on either the linear or quadratic polynomials describing temporal change in path shape.

Path shape and density

As ants explored a novel arena, they adjusted the shapes of their paths in response to the density of ants in the arena. Paths were more tortuous when ants were more crowded; turning index increased with overall density. This result is consistent with the predictions of theoretical work showing that a high turning index detracts from discovery rate at low densities, but not at high densities.

Turning index was correlated with density (average $r_s=0.61$, $\text{SE}=0.236$; corrected $r=0.475$, $P<0.02$). Turning index tended to increase with density. In eight of nine colonies r_s was positive; in four of nine colonies, it was 1 (Table I).

Figure 5 shows the relation between path shape and density in Small, Medium and Large colonies. At lower densities, turning index was lower than at high densities. Out of the nine colonies, the one exception to this trend was the Medium colony (Fig. 5b), represented by circles, which had a lower turning index in the Small arena (smallest circle) than in the Large arena (largest circle). Smaller symbols, representing smaller arenas, tend to be on the right in all three figures, because densities were higher in smaller arenas. Note that densities were highest for the Large colonies, especially in Small arenas (Fig. 5c); in Small and Medium colonies density was never higher than 0.4 ants per cm^2 , whereas in Large colonies density reached 1 ant per cm^2 (Fig. 5a, b).

The variation in turning index among ants did not appear to increase or decrease with density (Fig. 6). One would expect more variation at low

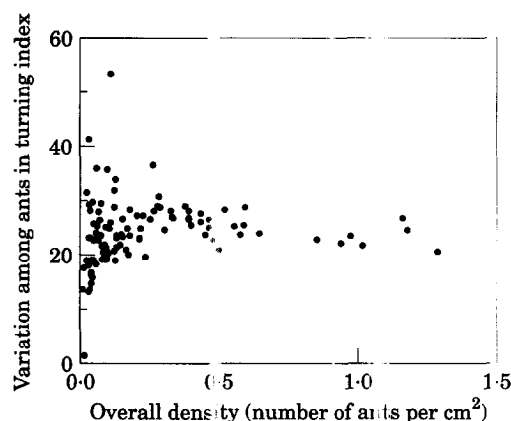


Figure 6. Standard deviation (over all ant paths) of turning index (over all steps within a path), as a function of density. Each point shows, for one of the 108 videotapes, the variation among ant paths in turning index.

density, simply because low densities mean a smaller sample of ant paths, and for many distributions, the smaller a random sample, the greater the variance of that sample. In addition, ants occupied the new arena at low densities more often than at high densities, so there are more data points at the low-density end of Fig. 6. Both of these factors combine to show a greater spread in turning index at low, rather than high ant density (Fig. 6). On average, however, there was no indication that variation in path shape among ants increases or decreases with density. Because of this, in the statistical analysis described above,

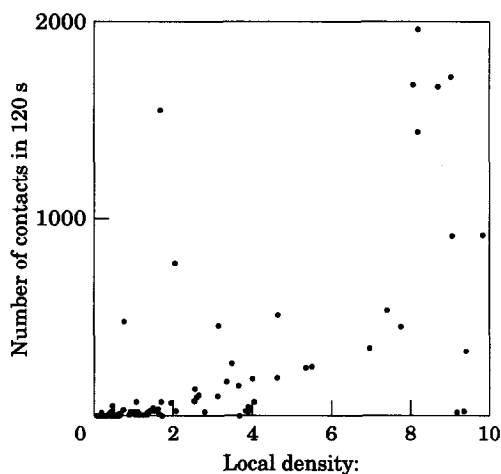


Figure 7. Encounter rate as a function of local density. Each point shows, for one of the 108 videotapes, the number of times that unique combinations of two or more ants came into contact. Density is measured as the number of ant paths tracked per cm² of the region analysed (see text).

turning index was averaged over all ant paths, and this mean was examined as a function of density.

Encounter rate and density

The total number of encounters observed in 120 s of filming appeared to increase quadratically with local density (Fig. 7). This result should occur if encounter rate is a consequence of

Table II. Difference in rate of spread after 5 and 20 min of exploration

Exploration time	Colony size	Spread into annulus between small and medium arenas			Spread into annulus between medium and large arenas		
		Difference	SE 5	SE 20	Difference	SE 5	SE 20
60–1 s	Small	0.6	2.4	1.9	5.5*	1.4	2.2
	Medium	3.1	2.8	2.6	4.9	1.7	2.6
	Large	20.5*	3.5	3.4	20.2*	6.9	6.0
120–60 s	Small	5.5	3.4	0.9	1.5	1.8	1.4
	Medium	1.1	2.6	2.4	0.5	1.5	2.8
	Large	12	7.5	3.5	0.6	3.0	2.9

'Difference' shows the mean difference in numbers of ants spreading from a smaller arena to a larger one. Differences are between numbers spreading out after 5 and after 20 min of exploration of the smaller arena. Rates of spread were calculated by comparing numbers of ants that had spread into the larger arena from 1 to 60 s, and from 60 to 120 s, after ants had access to the larger arena. SE 5 and SE 20 = standard errors of the rates of spread at 5 and 20 min, respectively.

*Difference significantly greater than zero (confidence interval for difference between means, $P < 0.05$).

random collisions. Thus, there is no indication that collision rate is non-random.

Temporal Change in Rate of Spread

Ants spread out more quickly in the earlier part of the exploration process. The rate of spread was always greater when ants had been in the arena 5 min than for 20 min (Table II). This trend held true for all three colony sizes, for both arena size transitions (spread from Small to Medium arena and from Medium to Large), and for both time intervals (from 1 to 60 s, and from 60 to 120 s, after ants had access to the larger arena). These differences were strongest in the first 60 s after the boundary was removed. Differences were statistically significant for this time interval for Large colonies, spreading both from Small to Medium and from Medium to Large arenas, and for Small colonies spreading from Medium to Large arenas (Table II). Rates of spread from 60 to 120 s after ants had access to the larger arena were not significantly different after 5 and 20 min.

DISCUSSION

As Argentine ants explore a novel space, the shapes of their paths depend on worker density. The relation between path shape and density is consistent with theoretical predictions (Adler & Gordon 1992) for how a group of searching ants might maximize discovery rate: paths are more linear when density is low. When each individual adjusts the shape of its path to the overall density of exploring ants, the likelihood increases that some ant in the group will find anything worth discovering in the region explored. This result provides an intriguing new example of the ways in which individuals, each acting independently and not subject to any central or hierarchical control, can coordinate group-level behaviour.

Argentine ants show a higher turning index when density is high. At low density, when tortuous paths can detract from the rate at which events are discovered, the ants use straighter paths. At high density, when tortuous paths do not detract much from discovery rate, the turning index increases.

There may be some benefits to winding or tortuous paths, which make paths of this shape useful when the density of searching ants is high

enough to offset their cost for discovery rate. For example, when the turning index is high, ants are likely to remain close to each other or collectively close to the same place, such as a food source. Observations of Argentine ants suggest that when a food source is discovered, some ants retrieve it, while others immediately begin to explore the region adjacent to it, thus forming a slowly spreading wave around it. A high turning index would be useful in an environment where food sources tend to be close together, because having found one food source, a tortuous path would tend to keep exploring ants nearby where they would be likely to find another. On a larger spatial scale, a high turning index would keep exploring ants closer to the nest than a straighter path shape, simply because a straighter path shape would take each ant a greater linear distance.

How does an individual ant assess density? One possible cue is the rate at which an ant contacts other individuals (Gordon et al. 1993). Another possible cue is amount of pheromone emitted by other ants; each ant present might contribute to some total amount perceived by every ant. In another ant species, rate of contact proved more important in assessment of worker density than total numbers of ants present (Gordon et al. 1993), but species may differ in this respect. A third possible cue is the amount of pheromone deposited on the surface that ants are walking on (Hölldobler & Lumsden 1980). Studies of the formation of foraging trails by Argentine ant colonies show that the amount of trail pheromone may reflect worker density (Aron & Pasteels 1989; Aron et al. 1989; Deneubourg et al. 1990). In the present study, however, ants spread throughout the novel arena, without forming a trail, in all 108 videotapes, which is not surprising because there was nothing for a trail of foragers to retrieve. The ants' behaviour indicates that they were not using trail pheromone, but they did adjust path shape to worker density. Further work is needed to establish what cues individuals use to make this adjustment.

If contacts between ants are the result of random collisions, the total number of contacts should increase quadratically with number of ants. There is no indication that contact is non-random in Argentine ants (Fig. 7). Recent theoretical work explores the possibility that contact rate is a cue in decisions about task allocation, and suggests that a colony can exploit its environment most

effectively by curtailing contact rate at high densities (Pacala et al., in press). This occurs in the ant *Lasius fuliginosus* (Gordon et al. 1993). Argentine ants form diffuse supercolonies, consisting of many nest aggregations that each contain reproductives and workers (Passera & Keller 1992). New nest associations form when reproductives and workers bud off from existing ones (Keller et al. 1989), perhaps when numbers of ants become too large. Perhaps in this species, the density of exploring ants from one nest association rarely becomes so high that it is useful to regulate contact rate.

Interesting, though weak, temporal patterns suggested that ants may change their path shapes over the course of 40 min of exploration of a novel region. In the first experiment, the linear component of turning index from 5 to 40 min tended to be negative; this indicates that the turning index decreased over time as density increased. The results of the first experiment, considered together with those of the second experiment on rate of spread, support this same trend. The number of ants exploring arenas in the first experiment increased significantly over time, which implies that densities were higher at 20 min than at 5 min. In the second experiment, when spread was measured, ants in Large colonies spread more rapidly at 5 min in an arena than at 20 min (Table I). Because the initial conditions (before arena boundaries were removed in the spreading experiment) were identical in both experiments, ants in spreading experiments probably increased in density from 5 to 20 min, as they did in the first experiment. Ants would be expected to spread more when the turning index was low, because they would tend to travel further in the same direction before covering ground already explored. Thus a greater rate of spread at 5 min than at 20 min implies that at 5 min, when density is lower, ants' paths have a lower turning index. Further work is needed to determine how quickly an ant may appraise the density of the group of exploring ants, and how quickly an ant may adjust its path shapes accordingly.

The network of paths created by a group of searching ants is expandable. It behaves like a net made of strands that relax and curl when the net is not being stretched. When density is high, or a large network is packed into a small space, each strand takes on a convoluted shape. When the network expands out to fill a larger space, each

strand stretches to a shape more like a straight line. These adjustments are accomplished by individuals that are not capable of appraising the state of the whole network, but as a result of its expandability, the network's capacity to encompass new events is enhanced.

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