GROUP-LEVEL EXPLORATION TACTICS IN FIRE ANTS

by

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This paper reports on an investigation of the patrolling system of the red imported fire ant, *Solenopsis invicta*. Most research on the behavior of ants outside the nest has been concerned with foraging, the search for and retrieval of food. Patrolling or scouting behavior in ants has not received as much attention, but it has been observed in several species (*e.g.* HÖLLDOBLER, 1981; HÖLLDOBLER & LUMSDEN, 1980). For example, in harvester ants (*Pogonomyrmex* spp.), patrollers are a distinct class of individuals that inspect the area immediately surrounding the nest and foraging trails, and respond to new food sources and disturbances (GORDON, 1984, 1987); they will also defend the nest against intruders (PORTER & JORGENSEN, 1981).

The home range of an ant colony may be divided into several functional regions. There are: 1) the nest, which houses the queen, brood and attendant workers, and may also house stores of food; 2) the local nest area, a mound or region whose structure is maintained by the colony, in which a disturbance will elicit an immediate reaction from an active colony; 3) the area under regular surveillance, or colony "territory" (*sensu* HÖLLDOBLER & LUMSDEN, 1980), in which the colony forages for food and

which the colony may defend; and 4) a zone at the margin of the home range that colony members will enter occasionally. The boundaries of these regions are subject to change. The fact that colonies respond quickly to new food sources, intruders, or other disturbances within their territories implies the existence of a patrolling system. There is a great deal to be learned about how such systems function.

This study investigates one aspect of the patrolling system in *S. invicta:* how a colony incorporates a novel space, which is at first entered only occasionally, into its territory, that is, how marginal regions (no. 4) become part of patrolled territory (no. 3). I recorded from films the paths taken by ants on small platforms introduced into laboratory colonies. Successive records were made over the course of several hours. I examined how the paths change as the colony enters, explores and patrols the novel space.

The fire ant was chosen for this study because *S. invicta* is an extremely territorial species (WILSON *et al.*, 1971). Since its introduction into the southeastern U.S. about fifty years ago, the species has spread very rapidly. It appears that when new foraging and colonizing sites open up, fire ants are especially adept at appropriating them (BUREN *et al.*, 1978; WILLIAMS, 1986). These observations at the ecological level suggest that on a short, behavioral timescale, the species is especially skilled at that aspect of patrolling under investigation in this study: exploring and occupying new areas.

There has been considerable interest in the movement patterns of foraging insects, including ants (*e.g.* HARKNESS & MAROUDAS, 1985) and other insects (SOLTZ, 1986; LE BOURG, 1985). LEONARD & HERBERS (1986) were able to characterize two ant species according to the tempo of foragers' movements. Most previous work on this subject seeks to establish a relation between spatial patterns of foraging and the foraging success of individuals. Here I examine whether there are any long-term patterns, in time or space, in the ways groups of patrollers move when exploring new areas.

To investigate group-level patterns of patrolling behavior, I ask: Is the behavior of individuals in the novel space constrained by colony-level behavior? A null hypothesis is that each individual simply wanders independently of the others, responding to whatever cues it finds. The existence of any repeatable group-level patterns in time and space would show that in addition, the wanderings of individuals are constrained by the social organization of patrolling.

Methods and results

1. Deriving the path types.

Seven monogynous colonies of *S. invicta*, 1-3 years old and containing 600-2000 individuals, were used in this study. All colonies were kept in the laboratory in plastic rectangular boxes ($30 \times 22 \times 10$ cm), the sides of which were coated with Fluon. The brood, queen and attendant workers stayed in test tubes filled with water and plugged with cotton. The ants were fed crickets and Bhaktar-Whitcomb (1970) diet.

All observations were made from film. Ants were filmed in the laboratory using a Photosonics 1Pl 16 mm high-speed camera and Nikon 105 mm micro-nikkor lens, at 24 frames/sec. The paths of ants were traced onto clear plastic sheets using a Movieola flatbed editing bed which made it possible to control the speed at which the film showed.

Several series of preliminary films were made. In the first series, films were made of ants walking on glass, sand and paper surfaces. I saw no appreciable differences. In subsequent films, the surface that ants walked on was covered with clean paper at the beginning of each filming session. A second preliminary series showed that path orientation was not strongly determined by laboratory conditions such as the location of lights or characteristics of the boxes in which ants were placed. This question was of general interest even though path orientation was not considered in detail in subsequent observations.

In a third preliminary series of films, I derived a standard procedure for making and transcribing films, which was used in all subsequent observations. A piece of glass ($11 \times 11 \times 0.6$ cm) covered with clean paper was placed on a pedestal consisting of a size 11.5 rubber stopper, in the colony's original nest box. The glass and pedestal, or "platform", were placed in the foraging area of the nest box, away from the nest tubes. Any ant in the colony had access to the pedestal and could thus crawl onto the platform. Thus the colony, not the experimenter, "decided" which ants would patrol the novel space of the platform.

The area filmed was most of the upper surface of the platform, filmed from above. An ink line of known length was drawn on the paper surface of each platform to calibrate distances walked in the film. Exploration of the platform surface was filmed at four time stages, in minutes elapsed since the platform was introduced: 30, 105, 180, 255 (75-min intervals). In all trials, by 255 min, the density and behavior of ants on the platform appeared no different from that in the rest of the foraging area in the nest box. That is, the platform appeared to be incorporated into colony territory. Thus 255 min was chosen as an arbitrary endpoint of the exploratory process investigated in this study. The transcriptions do not specify which end of the path the ant started from. In transcribing a path, the speed of the ant's movement was recorded by making a dot, or "step" every ten frames (0.41 s). The path was derived by connecting the dots, taking care when doing so to follow the actual path of the ant as much as possible.

In the third preliminary series of films, I made 6 10-s films of each of 3 colonies. In these 18 film segments, all paths visible for more than three "steps" were traced in 18 10 s film segments, comprising 6 segments from each of 3 colonies. In the course of tracing paths in all 29 preliminary film segments described above, I derived a classification of paths into 4 types, based on frequencies of: Antennal contact (ant touches the antennae of another ant and they move antennae together in a drumming motion); Antennal check (one ant touches the body or head (not antennae) of another ant, and no antennal contact follows); and Standing still, grooming (an ant remains motionless, or stands in one place grooming itself or grooming a nearby stationary ant).

The four path types are defined as follows. Type I. Frequent antennal contacts with other ants; two or more antennal contacts per path.

Type II. Ant stays still more than 10 frames (0.41 s) at least twice in the 10 s segment. The ant moves slowly, initiates no antennal contacts and performs no checks.

Type III. Ant moves in a slow meandering path, usually 3-6 or more steps per actual centimeter walked (6 steps/cm is a speed of 0.41 cm/s). It engages in frequent antennal checks, especially with ants of path type II. One or less antennal contacts.

Type IV. Ant's path is direct (few turns) and rapid (often three or less steps per cm, or 0.81 cm/s, except when ant passes through a region congested with other ants). One or less antennal contact or antennal check.

Any path could be classified as one of these four types. Path type III is the most loosely defined of the four, so there was a tendency for paths whose type was not obvious to be classified as Type III.

Each tracing of the paths seen in a particular segment of film can be considered a sample of the colony's behavior at that time. To insure that the sampling technique was reliable, I made 4 transcriptions of the same film segment, using a procedure that was followed in all subsequent films. Only paths of more than five steps were counted. If there were less than 40 ants in the first frame of the film, all paths of these 40 were transcribed. If there were more than 40, 40 were chosen by making a line at 1 inch vertical intervals across the picture (starting from the left-hand edge of the transcription) at the beginning of the film segment, and choosing every other ant along the line. In different transcriptions of the same segment, sampling lines were 1/4 inch apart, so that different transcriptions showed the paths of different ants. There were no significant differences among the 4 samples in the distribution of paths assigned to the four different types (chi-squared = 0.453, 3 df). Data used in the test are shown in Table 1.

Fig. 1 shows a transcription of one film segment. All four path types are included.

TABLE 1. Comparison of different tracings from a single film segment

| Samples | Path type | | | |
	I	II	III	IV
1	8	10	10	12
2	6	8	9	9
3	6	8	10	10
4	6	10	10	10

The table shows counts in each of four path types. Each sample is from a different tracing; all tracings were made from the same film segment. See text for definition of path types and description of transcription methods.

2. Patterns of patrolling behavior.

a. *Temporal pattern.*

In each of 7 colonies, I filmed the exploration of introduced platforms at the four time stages as above (30, 105, 180 and 255 min after platforms were introduced), making 28 (7 colonies × 4 time stages) 10 s film segments. In order to keep constant any effects of colony hunger level on patrolling behavior, all colonies were fed a large piece of Bhaktar-Whitcomb diet a half hour before filming. The paths were traced and
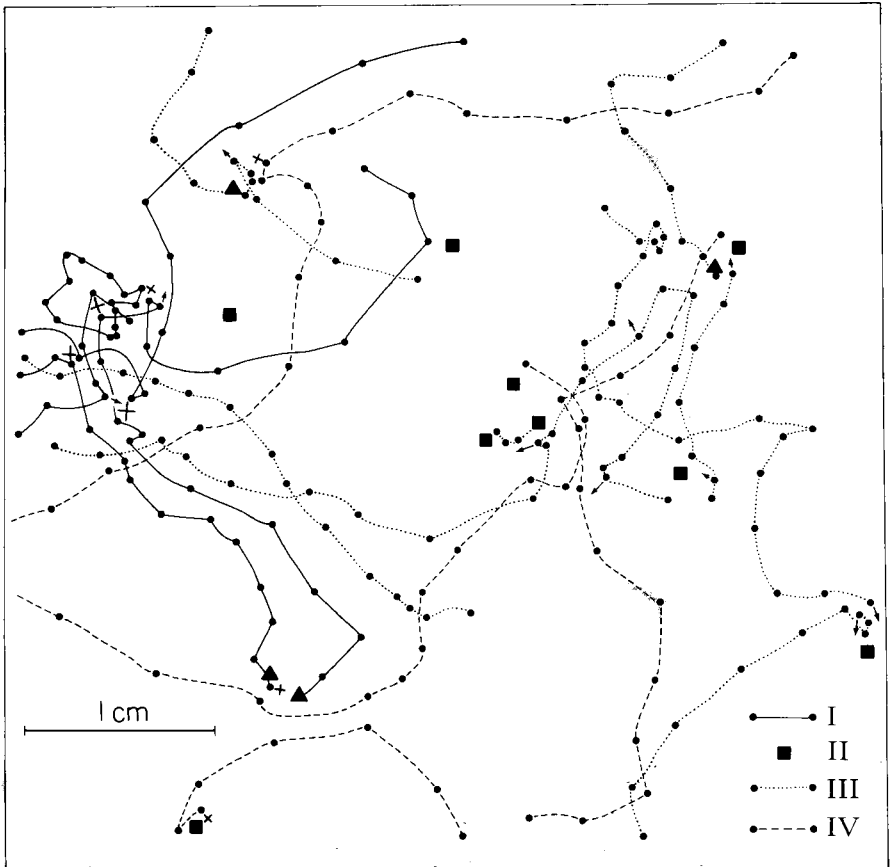
Fig. 1. Tracing from one 10-sec film segment. Shown are all paths in one sample tracing of a 10-sec film segment. Roman numerals refer to path types. x = antennal contact, small arrow = antennal check. Both paths involved in an antennal check or antennal contact may not be shown because recipient was not included in sample.

classified into 4 path types as described above. Figure 2 shows the mean number of paths of each type, as a function of time since the novel space was introduced.

A three-way G-test of heterogeneity (SOKAL & ROHLF, 1969) was performed to test whether path types were randomly distributed across time stages. The results are shown in Table 2. The distribution of path types was significantly non-random overall, and there was a highly significant time stage × path type interaction. Colonies also differed significantly in
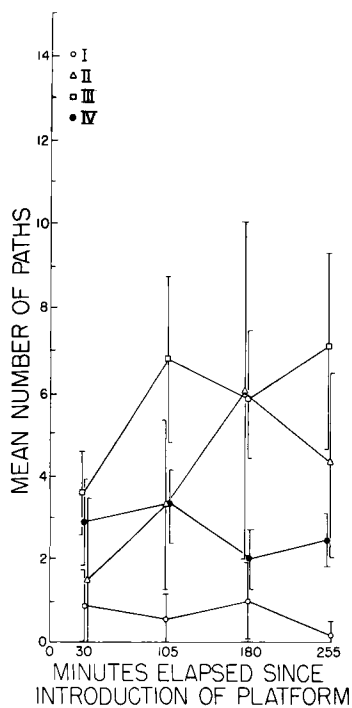
Fig. 2. Temporal patterns of distribution of paths into four types. Shown are the mean numbers of paths of each type, countes in tracings of 32 10 s film segments. Roman numerals refer to path types. The abscissa is the number of minutes since a platform was introduced into the nest box. Error bars show the standard errors of the mean.

TABLE 2. Test for temporal patterns in distribution of path types

Effects	DF	P
Overall	99	0.001
Path type × Time stage	9	0.001
Time stage × Colony	**18**	**0.05**
Colony × Path type	**18**	**0.001**

The table shows the results of a G-test of heterogeneity in which factors were colony, time stage and path type. Df = degrees of freedom.

their tendency to exhibit each path type at each time stage, perhaps because of differences in colony size, though the time stage × colony interaction was barely significant at the 0.05 level. In general, the results show that there is a clear temporal pattern in the tendency of patrollers to use paths of different types in the exploration of a novel space.

b. *Individual path specificity.*

Fire ants show considerable size polymorphism. To test whether individuals of particular size correspond to particular path types, I removed individuals in each type. Size was estimated by measuring head width. Sample sizes are shown in Table 3. Platforms were set up as in the filming procedure described above. I could see all of the platform when observing it directly, while most, but not all of it was visible on film. Because I could observe directly a path of longer duration than was visible on film, criteria for selecting ants engaged in each path type were made more stringent. The criteria were: in the entire path of an individual across the upper surface of the platform: Type I, >4 antennal contacts, Type II no movement, no checks or antennal contacts, Type III slow, <2 antennal contacts or checks, Type IV fast, no antennal contacts.

Head widths were measured dorsally, using an ocular micrometer, as the distance between the most widely separated points on the compound eyes. Table 3 shows the mean head widths and sample sizes for each path type in different colonies. Ants removed while walking Type I paths were invariably the largest; those removed while walking type II paths usually

TABLE 3. Mean head widths by path type

| Samples | Path type | | | |
	I	II	III	IV
1	0.671	0.664		
	(9)	(5)		
2	0.722	0.609	0.696	0.647
	(10)	(10)	(6)	(10)
3	0.693	0.646	0.600	0.689
	(11)	(10)	(10)	(10)
4	0.688	0.580	0.609	0.639
	(8)	(10)	(9)	(11)

The table shows the number of individuals measured (in parentheses) and the mean head widths, for each colony and path type. In colony 1, no ants were sampled walking path types III and IV.

(except for colony 3) the smallest; and those of either type III or IV paths the 2nd and 3rd largest. These head widths are among the smallest classes found in *S. invicta*; most workers that went onto the platforms were minor workers.

A two-way ANOVA was performed on measurements of head widths, with path type and colony as main effects. Results are shown in Table 4. Colonies differed in head widths; the distribution of worker sizes clearly depends on colony age and other colony-specific factors in fire ants (WOOD & TSCHINKEL, 1981; PORTER & TSCHINKEL, 1985). The most highly significant effect was that of path type, showing that individuals of particular sizes do tend to fall into particular path types. There was a significant colony × type interaction, showing that the distribution of sizes into path types differs across colonies.

TABLE 4. Size polymorphism by path type

Effects	SS	DF	F	P
Colony	2.922	2	4.2	0.018
Path type	12.945	3	12.3	0.0001
Colony × Path type	5.322	6	2.5	0.025
Error	36.117	103		

The table shows the results of an ANOVA using measurements of head width, in which colony and path type were main effects. SS = sum of squares, DF = degrees of freedom, F = F-ratio.

4. Perturbation experiments.

a. *Presence of food.*

A series of films was made as before using 4 colonies, at the same 4 time stages. A piece of filter paper with a dab of peanut butter on it was placed at the corner of each platform. Fig. 3 shows the means of the resulting counts of path types. The presence of food increased the overall activity level on the platform. The most obvious result was the sharp increase of Type I paths. Ants visiting the food engaged in very frequent antennal contacts with ants approaching the food (Fig. 4). One function of antennal contacts is apparently to transmit information about the presence of food.

b. *Removals.*

Two perturbations were done to determine whether the extent to which ants in one path type accomplish their task affects the behavior of ants
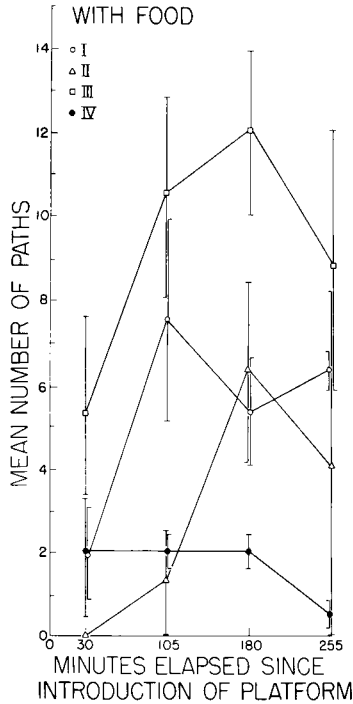
Fig. 3. Temporal patterns of path types, in the presence of food.

of other path types. In the first, in each of two colonies, 11-13 ants walking Type I paths were removed between 30 and 100 min after the introduction of the platform. In the second, in each of two colonies, 7-10 ants walking type II paths were removed. Removals were made with a narrow-tipped aspirator and caused no apparent disturbance. Criteria for removals were the same as those used in removals for measurements of head width described above. In all 4 colonies, paths were filmed at 4 time intervals as before.

Figure 5 shows the results. Removing ants walking Type I or II paths caused a clear decline in numbers of Type II paths. When ants walking Type I paths were removed, the peak of numbers of Type II paths shifted from 180 min when there were no removals (Figs 2 and 3) to 105 min, and there was some decline in the numbers of Type IV paths. When ants walking Type II paths were removed, numbers of Type I and IV paths also declined. The results of measuring ant head widths show that dif-
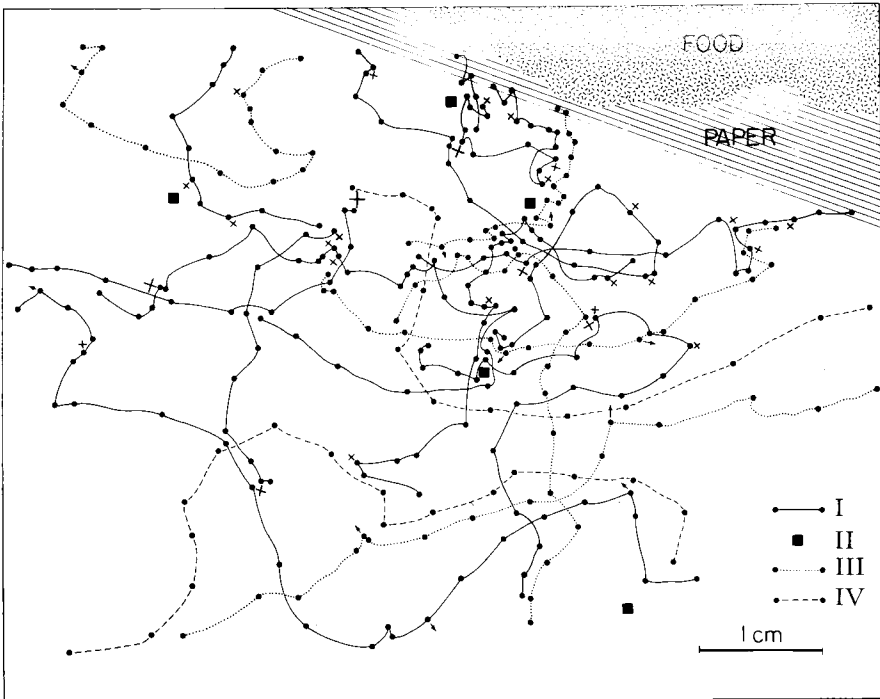
Fig. 4. Tracing from one 10-sec film segment, when food is present. Shown are some paths from one sample tracing of a 10-sec film segment. Food was placed in one corner of the nest box. x = antennal contact, small arrow = antennal check.

ferent path types are performed by different classes of individuals. The results of the removal experiments suggest that the behavior of one class is affected by the behavior of other classes.

Discussion

When a fire ant colony explores a new region, the process is subject to clear spatiotemporal patterns. Members of distinct classes of individuals, of different head widths and body sizes, move in distinct ways. Members of one class or type engage in antennal contact with many of the other ants they encounter. Members of a second class come into the new region and then remain almost stationary. Members of a third class move slowly through the region, inspecting the slow and stationary ants. Members of a fourth class move rapidly and directly through the region, not engaging in antennal contact with other ants.
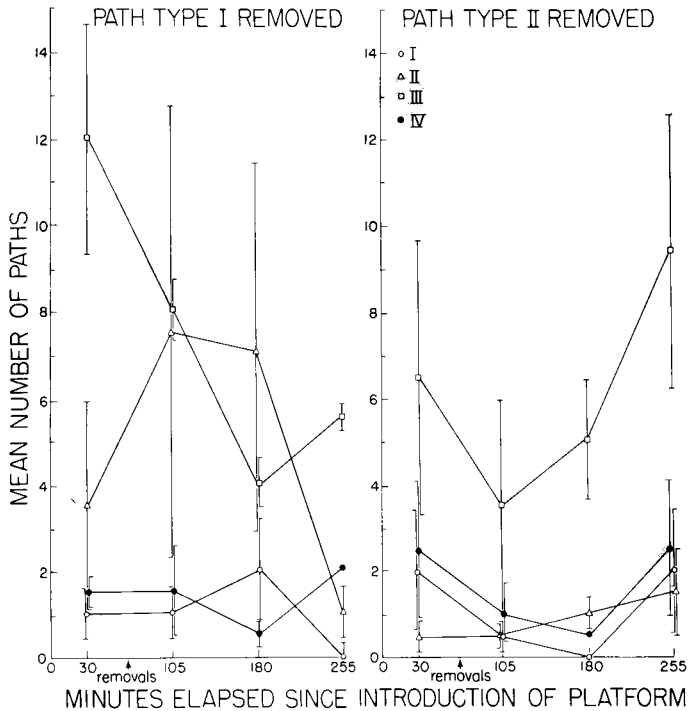
Fig. 5. Temporal patterns of path types, after individuals of one type were removed.

The behavior of these four classes of ants is temporally patterned. At successive stages of the exploration, significantly different frequencies of each type are present in the new region. Disruption of the temporal pattern changes the frequencies with which ants of any type appear on the platform. Further perturbation experiments are needed to investigate how the behavior of patrollers depends on that of patrollers of other types.

It is difficult to relate the present results on size polyethism to the existing literature, because patrolling and exploration have not been studied in detail in previous investigations of division of labor in *S. invicta*. All four types of workers coming on to the platforms are among the smallest in the colony. Their mean head widths, ranging from 0.588 to 0.722 mm, correspond to those of the minors or smallest size classes described in previous work (*e.g.* WILSON, 1978; MIRENDA & VINSON, 1981). MIRENDA & VINSON (1981) showed that minor workers are more

likely to engage in brood care early in their lives, but appear in foraging areas at a younger age than larger workers do, and that minors are less likely than larger workers to retrieve insect prey but more likely to retrieve liquid prey. The present results suggest that various subclasses of minor workers may be patrollers.

Type I patrollers, the subclass with the largest head size, which engage in frequent antennal contacts and which increase in number when food is present, may be the ones that find new food sources and recruit the colony to them. Many students of ant behavior have been struck by the ubiquity of antennal contacts, and such contacts may play a role in greeting, in eliciting trophallaxis, or in the recognition of non-colony members (WILSON, 1971; KISTNER, 1966). The social function of antennal contact is not yet fully understood. The present study suggests that recruitment to food may use information transmitted through antennal contact as well as trail pheromones emitted through abdominal glands.

It is tempting to regard Type II paths as evidence of sentry-like behavior. Type III paths involve frequent checks of Type II ants; perhaps this group of patrollers collects information from the Type II "sentries". This will have to be investigated in further studies. It is not clear whether ants making Type IV paths contribute to the patrolling system. Numbers of Type IV paths seem relatively unaffected by perturbations, though the numbers of this type declined when types I and II were removed. Type IV paths may be those of ants that happen to be passing through the novel space, and who take an alternate route if normal exploration is disrupted and alters the status of the platform. The function of differences in body size, in the four types of patrollers, remains to be investigated.

Group-level coordination of foraging movements has been of interest in efforts to distinguish "group" and "individual" foraging strategies (e.g. DAVIDSON, 1977), but it is difficult to establish spatial coordination among group members through an analysis of their paths. In statistical mechanics and in the theory of random walks, there have been attempts to predict the behavior of collections of moving particles, such as the amount of area covered, based on characteristics of the particle's movement (e.g. amount of turning, overall directionality) (BERG, 1983; SPITZER, 1964). Eventually such theory should make it possible to predict, for example, where and how often ants moving in particular ways would encounter each other. In a series of computer simulations, made in collaboration with M. KARDAR, I found that the path types observed in this study could be replicated using a very simple model.

Such models could be used to investigate further the functions of the 4 path types, by examining how spatial coordination between individuals differs in groups walking each type of path.

This work opens up many new questions about fire ant behavior. *S. invicta* explores a novel space using a temporally patterned series of diverse path types. Certain classes of individuals tend to play particular roles in this process. A colony's exploration of a new space is not merely implemented by each individual's independent response to chemical cues, but also by individual participation in group-level patterns of patrolling behavior. These group-level processes may involve a system of information exchange that could help to account for the territorial dominance of *S. invicta*.

Summary

This study investigates how fire ant (*Solenopsis invicta*) colonies explore and patrol a new region. Small platforms were introduced into nest boxes of laboratory colonies. The paths of ants walking on the platforms were filmed at 30 min after the platforms were introduced, and at 3 75-min intervals thereafter. The results showed:
1. There are four distinct path types used by patrollers in the new region. The different types vary with respect to speed, number of antennal contacts, and the extent to which paths maintain a single direction.
2. Head widths of individuals differ significantly according to path type.
3. In the course of several hours after the new region is introduced, there is a temporal pattern in the numbers of paths of each type.
4. Removal experiments suggest that temporal patterns in the numbers performing on, path type, depend on numbers previously performing other path types.
5. The behavior of individuals exploring a new region is constrained by colony-level patterns of behavior.

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Zusammenfassung

In diesem Aufsatz wird untersucht, wie Ameisengruppen der Art *Solenopsis invicta* ein neues Gebiet erforschen und abpatrouillieren. Kleine Plattformen, hergestellt aus einer flachen Glasscheibe auf einem Postament, wurden von uns in die Nestkisten der Laborgruppen von *S. invicta* eingebracht. Die Pfade der auf den Plattformen gehenden Ameisen wurden dann verfilmt, 30 Minuten nach dem Einführen der Plattformen und danach in drei Zwischenräumen von jeweils 75 Minuten. Die Ergebnisse sind die folgenden:

1. In dem neuen Gebiet bildeten die patrouillierenden Ameisen vier verschiedene Pfadtypen. Die verschiedenen Pfadtypen unterscheiden sich voneinander in Bezug auf die Geschwindigkeit der Ameisen, die Zahl der Fühlerberührungen und die Richtung der Pfade (d.h. in wiefern hält der Pfad eine Richtung ein).

2. Die Kopfbreiten der die vier Pfadtypen ausführenden Einzelameisen sind in einer statistisch bedeutsamen Weise unterschiedlich.

3. Im Laufe mehrerer Stunden nach der Einführung des neuen Gebietes entsteht ein deutliches zeitliches Muster in der Zahl der einzelnen Pfadtypen.

4. Nach Entfernung einiger Tiere zeigte sich, dass dieses Muster davon abhängt, wieviele Tiere vorher andere Pfadtypen gegangen sind.

5. Die Verhaltensmuster im Gruppenebene zwingt das Verhalten von Individuen die ein neues Gebiet erforschen.