Information Collection and Spread by Networks of Patrolling Ants
Author(s): Frederick R. Adler and Deborah M. Gordon
Reviewed work(s):
Source: *The American Naturalist*, Vol. 140, No. 3 (Sep., 1992), pp. 373-400
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2462773
Accessed: 30/01/2012 14:46

INFORMATION COLLECTION AND SPREAD BY NETWORKS OF PATROLLING ANTS

FREDERICK R. ADLER* AND DEBORAH M. GORDON†‡

*Center for Applied Mathematics and Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853; †Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, United Kingdom

Abstract.—To study how a social group, such as an ant colony, monitors events occurring throughout its territory, we present a model of a network of patrolling ants engaged in information collection and dissemination. In this network, individuals follow independent paths through a region and can exchange signals with each other upon encounter. The paths of the ants are described by correlated random walks. Through simulations and analytic approximations, including a new approach to the spatial logistic equation, we study the efficiency with which such a network discovers a constantly changing stream of "events" scattered throughout the region and the speed with which information spreads to all ants in the network. We demonstrate that efficiency of event discovery and the speed of information spread are enhanced by increased network size and straighter individual ant paths, and that these two effects interact. The results lead to predictions regarding the relations among species-specific movement patterns, colony size, and ant ecology.

Ants perform a variety of tasks outside their nests. The most familiar is foraging: collecting food and bringing it back to the nest. This task actually involves two components, food discovery and food collection. Models of foraging have focused either on individually foraging ants that both discover and collect food (Bovet 1981; Goss et al. 1989) or on individually searching ants ("scouts") that recruit specialized food collectors (Taylor 1978; Harkness and Maroudas 1985; Johnson et al. 1987; Pasteels et al. 1987). The discovery of food is one important outcome of an ant colony's efforts to monitor its environment, but colonies discover other kinds of events as well, including new nest sites, ants of other colonies and species, sources of danger, and so on. Here we consider the general problem of how an ant colony might maintain an ongoing flow of information about its environment.

We are especially concerned with modeling the consequences for information collection and spread by information-gathering ants that do not search in isolation but encounter each other and share information. Information-gathering behavior, called "scouting" or "patrolling," appears to be common in ants (although the literature on this is obscured by a tendency to assume that any ant outside the

‡ Present addresses: F.R.A., Department of Zoology, University of California, Davis, California 95616; D.M.G., Department of Biological Sciences, Stanford University, Stanford, California 94305.

nest is foraging, i.e., actively engaged in food retrieval). A variety of tasks under-taken by these ants have been documented. For example, in seed-eating ants (*Pogonomyrmex*), it is the patrollers, not foragers, that discover new food sources and recruit foragers to them (Gordon 1983). Each morning, furthermore, the pa-trollers explore the existing foraging trails to stable food sources. The trails cho-sen by the patrollers are used later in the day by the foragers (Gordon 1991). Patrollers react to other kinds of changes in the colony's environment, such as alterations in the nest structure and encounters with ants of other species (Porter and Jorgensen 1981; Gordon 1987). In fire ants (*Solenopsis invicta* Buren), the patrollers explore new regions before they are used by other members of the colony (Gordon 1988).

Information sharing among patrollers seems likely given the frequency of en-counters among them. Such encounters often involve antennal contact. Ants per-ceive chemical cues with their antennae. In the course of antennal contact, one ant may receive chemical information about the state of the other. For example, an ant may perceive that the one it contacts is carrying food, or that it is a nest mate (Lenoir and Jaisson 1982; Hölldobler and Wilson 1990). Waves of alarm are well documented, occurring when ants respond to an airborne pheromone by emitting more themselves (Bossert and Wilson 1963). It remains to be demon-strated empirically that an ant that receives a chemical signal from another in the course of a brief encounter can pass the signal on to a third. A recent study of the ant *Lasius fuliginosus* shows that these ants act to maintain relatively constant encounter rates as density changes, which suggests that reliable encounter rates may be biologically important (Gordon et al. 1992).

Here we develop a theoretical approach to the study of information spread through brief encounters, in the hope that such models will contribute to further empirical work. A group of workers that walk around and inspect the colony's foraging range while frequently encountering other workers can be viewed as a sort of network. Encounters act as the vertices of this network and provide the opportunity for ants to exchange information.

The effectiveness of patrolling depends on how exhaustively the network cov-ers the region occupied by a colony, how sensitive it is to changes in the environ-ment, and how well it disseminates information about such changes. An ant col-ony would have complete information about its environment if there were an ant everywhere at all times, and if any ant could communicate instantaneously with any other. Colonies must balance the cost of failing to achieve this ideal against the cost of supporting a large contingent of patrollers and the cost of communica-tion. Moving patrollers provide one potentially effective approach to this problem because each ant spends most of its time distant from other ants exploring terri-tory and only a small fraction of its time close to another ant to which it can potentially communicate its findings. The spatial pattern of individual patroller paths determines both the effectiveness of a patrolling network in covering the region occupied by the colony and the frequency and distribution of encounters. To take an extreme example, if each patroller traveled only on one straight line leading away from the nest, the region near the nest would be explored more frequently and patrollers might never meet. The frequency of patroller encounters

determines the speed with which information can spread through the network, and thus the time scale of events to which a colony can respond.

The model presented here has two objectives. First, we consider how patroller path characteristics and patroller number affect the efficiency with which a patrolling network explores a region. Second, we consider how patroller path characteristics and patroller number determine the rate and spatial pattern of information spread through a network connected by local contacts. In part, this extends work on the question of how an individual forager should move in order to search most effectively (Pyke 1978a, 1978b; Zimmerman 1979; Bovet 1981; Hoffman 1983; Dusenberry 1989; Stillman and Sutherland 1990) and more generally how a group of foragers might behave in order to search effectively as an ensemble (Cody 1971; Harkness and Maroudas 1985; Wehner 1987).

The general context of this work is the integration of simple individual behavior into more complex colony-level behavior. In biological systems, such integration must take place through some sort of information exchange. Two modes of exchange have received attention in the literature. In the first, exchange takes place directly between individuals only at a single central location, such as the nest (Pasteels et al. 1987; Goss and Deneubourg 1989; Beckers et al. 1990; Seeley et al. 1991). In these models, monitoring the status of individuals, such as the food source they use, does not require continuously tracking locations. In the second, information exchange takes place indirectly through modification of the environment, either through trails (Pasteels et al. 1987; Deneubourg et al. 1989; Goss and Deneubourg 1989; Beckers et al. 1990) or through nest characteristics (Camazine et al. 1990). Trail models are analogous to central place exchange models when the trails radiate from a single source at the nest. Beckers et al. (1990) used a common framework to compare these two modes of information exchange. Through simulation, Deneubourg et al. (1989) described the complex two-dimensional patterns that can be generated by a moving column of trail-producing army ants, and Camazine et al. (1990) demonstrated that the pattern of eggs, larvae, and honey in a comb can be generated simply by response of individuals to local conditions. We know of only one model (Frehland et al. 1985) that treats the problem of information dissemination through space. This model describes a system wherein alarm spreads through a network of sentries that remain stationary until they are alarmed.

Most previous models have been concerned with the effectiveness of discrete episodes of searching or the propagation of a single alarm. Our model is concerned with the more general problem of maintaining a stable network consisting of moving individuals that provide continuous information about a large region.

THE MODEL

Our model simulates two tasks undertaken by networks of patrolling ants: discovery of events (such as the appearance of food or danger) and dissemination of information. We do not here attempt to optimize behavior with respect to a particular fitness criterion with constraints (Johnson et al. 1987; Goss et al. 1989) but rather to study how the completion of particular tasks depends on the parame-

TABLE 1

PARAMETERS

Parameter	Description	Values Used
n	Number of ants	1, 30, 60, 100
r	Step length	1
σ	Standard deviation of turning angle	.5, 1, 2, 4
d_0	Radius of territory	25
w	Perceptual radius	1.5
μ	Mean event persistence time	50
m	Number of events	10
β	Reencounter avoidance parameter	0, 1

ters of the model. As in much foraging theory, we can then optimize the efficiency of single tasks in isolation, ignoring the fact that a strategy optimal for one task may be very inefficient for another.

Table 1 and figure 1 give a summary of the model parameters and model structure described below. The network consists of n identical ants, each executing a correlated random walk (Kareiva and Shigesada 1983), a sequence of steps with fixed step length r and with direction chosen from a linear normal distribution wrapped around the circle, with mean equal to the direction of the previous step and standard deviation σ. A larger mean square turning angle produces a path with sharper turns, and, if σ is greater than about 5, one has essentially a random walk with no correlation. See figure 1 for illustration of random walks with different values of σ. The normal formulation of the random walk can be justified as a sum over several steps of a more complicated random walk (Bovet and Benhamou 1988). We assume that ants' patrolling trajectories are not affected by chemical cues in the substrate. The ants remain in a circular region of radius d_0 centered at the nest and are constrained by a soft reflecting boundary region in which step directions are biased more and more toward the nest as ants move farther from it.

The existence of a reflecting boundary has two important implications that distinguish our model from previous models. First, some optimization models (Bovet 1981; Frehland et al. 1985; Harkness and Maroudas 1985) have shown that a high turning angle is necessary to keep ants from wandering far from the nest in the absence of a territorial boundary. Second, a reflecting boundary leads to roughly uniform coverage of the region by information-gathering ants, in contrast to the decreasing coverage with distance from the nest found in models without a reflecting boundary (Frehland et al. 1985; Harkness and Maroudas 1985; Goss et al. 1989). In another contrast with a previous model (Harkness and Maroudas 1985), our patrolling ants do not specialize in particular sectors. This is a consequence of the fact that we have assumed no memory in our ants, although this factor has been shown to have potentially important implications for ant foraging (Goss et al. 1989).

In our model patrollers interact with each other only through encounters, which occur when two ants move within a perceptual radius w of each other. We thus
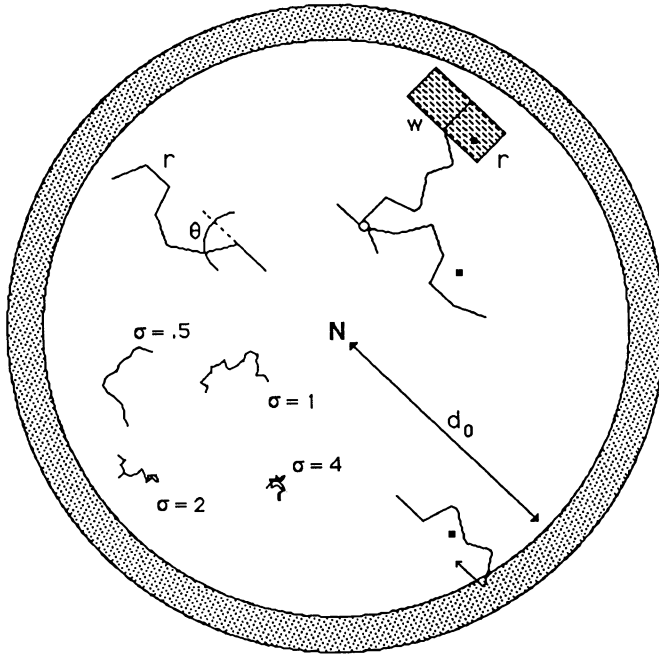
Fig. 1.—Overview of the model. The lines represent the paths of four ants, with turns taking place after steps of length r. The turning angle θ is drawn from a linear normal distribution of mean 0 and standard deviation σ wrapped around the circle. *Small solid squares* represent events that have been discovered, and the *shaded area* shows the area explored by a single ant during a single time step. The *small open circle* shows an encounter between two ants. The circle at distance d_0 from the nest is the boundary of the region, and ants begin to return toward the nest when they cross this boundary into the *speckled area* (the soft reflecting boundary), as illustrated by the ant in the lower right. Representative paths (ca. 15 steps long) of ants with four values of σ, the standard deviation of the turning angle, are also shown.

ignore long-range communication through pheromones. An encounter lasts a single time step, and the ants then depart with mean directions modified by the reencounter avoidance parameter, β, where $\beta = 0$ allows each ant to leave the encounter with mean direction unaltered by encounter, and $\beta = 1$ forces the two ants to leave the encounter with diametrically opposite mean directions. Intermediate values of β, not used in this article, can be used to interpolate between these two cases.

Empirical tests of the model require measurement of these parameters, which break into the two categories: parameters describing individuals and parameters describing the colony as a whole. Individual parameters include the step length, r; the standard deviation of turning angle, σ; and the perceptual radius, w. Some of these have been measured for some ant species in studies of the spatial behavior of individual foragers (Harkness and Maroudas 1985; Leonard and Herbers 1986), or of encounter rates among foragers and patrollers (Gordon et al. 1992). For example, Gordon et al. (1992) show that the perceptual radius for *Lasius*

fuliginosus is roughly 1.2 cm. Jutsun (1979) shows that the intraspecific perceptual radius of *Atta cephalotes* is roughly 0.8 cm, although these ants could detect *Acromyrmex octospinosus* at a larger distance of 1.5 cm. As for the colony-level parameters, the number of patrollers, n, could be estimated simply by counting, and the foraging range, d_0, and the contact avoidance parameter, β, could be estimated by observation.

The efficiency with which the network explores the region is studied through the following process. An ant discovers an "event," which can be thought of as a food item or a hint of danger, when it comes within the perceptual radius, w, of it. Upon discovery of an event, an ant departs with mean direction identical to direction of arrival (cf. Pyke 1978b). There are m events scattered randomly throughout the region that are immediately replaced at random upon discovery. Events also disappear for other reasons (to model processes such as removal by other species) with constant probability $1/\mu$ on each time step, leading to a mean residence time of μ for events not discovered by ants. We define the efficiency of ants at discovering events to be the fraction of events that are discovered by ants over the course of a long run and measure efficiency for a range of parameter values, focusing on the effects of turning angle and network size. For a given regime of event production and disappearance, this measure is equivalent to the standard rate of event discovery used in foraging theory (Stephens and Krebs 1986).

The spread of information through the network is studied as follows. A single ant is "informed" of or discovers some unspecified piece of information. We do not consider the consequences of a change in the behavior of an ant once it becomes informed, but this would not be difficult to add to the model. When an informed ant encounters another ant, it informs the other ant, which can in turn inform other ants. Two measures of information spread are followed over time: the fraction of ants informed (which increases monotonically to 1 because ants never forget in this model), and some measure of the area covered by informed ants. The two measures of information spread allow us to check whether there is a trade-off between rapid spread of information measured as the number of ants informed, and coherent spread measured by the concentration of ants informed in the neighborhood of the original information.

<div style="text-align:center">ANALYTIC APPROXIMATIONS</div>

Nonspatial Models

We derive several approximations of the processes of event discovery and information spread, to be compared later with simulation results. The approximations in this section ignore the spatial aspects of the process, with refinements in the subsequent section incorporating aspects of spatiality. Table 2 lists and describes the variables used in these approximations.

Null model of event discovery.—All approximations depend on various versions of a parameter λ, which represents the fraction of the region newly explored by a single ant during a single time step. This parameter then gives the probability

TABLE 2

VARIABLES

Variable	Description	Equation
i, j	Indices for ants	
λ_0	Maximum fraction of total area explored in one time step	(1)
ϕ_n	Expected fraction of events discovered by n ants ignoring effects of turning angle	(3)
$\hat{\phi}_n$	Approximate ϕ_n	(4)
T_n	Mean residence time of event in presence of n ants	(7)
$I(t)$	Nonspatial approximate number of informed ants	(8)
$\bar{\lambda}$	Corrected fraction of total area explored in one time step	(11)
$\hat{\psi}_n$	Expected fraction of events discovered by n ants including effects of turning angle	(12)
$\bar{I}(t)$	Spatial approximate number of informed ants	(16)
$\bar{S}(t)$	Spatial approximate number of uninformed ants	(16)
$A_I(t)$	Area taken up by informed ants	(16)

that an ant discovers a particular event during a particular time step. The simplest approximation, denoted λ_0, is the ratio of new area explored by an ant over the course of a single time step, $2wr$, to the total area, πd_0^2, or

$$\lambda_0 = \frac{2wr}{\pi d_0^2}.\tag{1}$$

This ignores the fact that ants that do not walk in straight lines lose efficiency both by searching the same area twice on consecutive time steps and by turning around and searching the same area multiple times after longer delays (Cody 1971; Pyke 1978a; Dusenberry 1989). Therefore λ_0 is an upper bound on the fraction of region effectively explored during a single time step. This model has been termed "random search" to contrast with "systematic search" (Dusenberry 1989).

Using λ_0, we can estimate the probability that an event is discovered by ants before it disappears because of other causes. Defining q_n to be the probability that at least one of n ants finds a particular event on a particular time step, we then have, because ants act in parallel during the course of a single time step,

$$q_n = 1 - (1 - q_1)^n,\tag{2}$$

where $q_1 = \lambda_0$ (Oster and Wilson 1978). Let $p = 1/\mu$ be the probability of spontaneous disappearance per time step and ϕ_n be the probability that the event is first found by one of the ants. Because of our assumptions of independence of discovery and disappearance, ϕ_n is the ratio of the probability that ants find the event on a given time step to the probability that the event is found or disappears on that time step. The probability that an event is found or disappears on a given time step is $1 - (1 - p)(1 - q_n)$, so

$$\phi_n = \frac{q_n}{p + q_n - pq_n}.\tag{3}$$

In the case where $n\lambda_0$ is small, we have

$$q_n \approx n\lambda_0,$$

in which case we can approximate ϕ_n by $\hat{\phi}_n$ as follows:

$$\hat{\phi}_n = \frac{n\lambda_0}{p + n\lambda_0}. \tag{4}$$

Noting that

$$\hat{\phi}_1 = \frac{\lambda_0}{p + \lambda_0},$$

we can compute $\hat{\phi}_n$ in terms of $\hat{\phi}_1$ as follows:

$$\hat{\phi}_n = \frac{n\hat{\phi}_1}{1 - \hat{\phi}_1 + n\hat{\phi}_1}. \tag{5}$$

This equation describes how efficiency scales with the number of ants, and it is interesting to compare it with the expression for ants acting in parallel described by Oster and Wilson (1978). Given that a single ant has probability of success ρ_1, n ants acting in parallel have probability of success ρ_n given by

$$\rho_n = 1 - (1 - \rho_1)^n. \tag{6}$$

If $\rho_1 = \hat{\phi}_1$, ρ_n increases to 1 as n increases much more rapidly than does $\hat{\phi}_n$. This diminished rate of increase in efficiency with increasing group size is not a consequence of the fact that events last multiple time steps, because one has exactly the form of equation (6) when the event lasts a fixed number of time steps. It is rather a consequence of the random disappearance of events due to other agents, and we thus term the scaling given in equation (5) the "random event disappearance" rule to distinguish it from the scaling given in equation (6), which we term the "constant event duration" rule. The difference between these two rules is due to the different way events interact with the environment, not to a different way that ants interact with the events or each other. The lower efficiency of ants experiencing the random event disappearance rule is thus not a consequence of interference or lack of cooperation among the ants. See Appendix A for further discussion of this issue.

We can also compute the expected residence time of an event in the presence of ants. Because the probability of event disappearance per time step is just $p + q_n - pq_n$, independent of the age of the event, the expected residence time will be the reciprocal of this. When both p and q_n are assumed to be small as above, this residence time, T_n, in the presence of n ants can be computed in terms of μ and ϕ_n:

$$T_n = \mu(1 - \phi_n). \tag{7}$$

Thus residence time is proportional to the fraction of events not discovered by ants.

Null model of information spread.—Using λ_0 as the approximate probability that a particular ant encounters another particular ant on a given time step, we

can find an approximation to the number of ants informed as a function of time. Letting $I(t)$ represent the number of ants informed on time step t, we then have

$$E(I(t + 1)) = I(t) + \lambda_0 I(t)(n - I(t)),$$

where E represents the expected value. The second term represents the expected number of ants informed during a time step and is the product of the number of pairs of ants that have exactly one informed member with the probability λ_0 that they encounter. Such systems are considered in detail by Bailey (1975) for models of epidemics. For the accuracy needed here it is sufficient to make two approximations: the first being to ignore the probabilistic elements of information spread, which is reasonable as long as neither $I(t)$ nor $n - I(t)$ is too small, and the second being to ignore the effects of discrete time steps, which is reasonable as long as the expected number of ants informed during a single time step is fairly small. Denoting the approximate version of $I(t)$ by $\hat{I}(t)$ we have

$$\frac{d\hat{I}(t)}{dt} = \lambda_0 \hat{I}(t)(n - \hat{I}(t)). \tag{8}$$

With the initial conditions that I_0 ants are informed at time 0, this logistic equation is easily solved, and predicted trajectories can be compared with simulated trajectories. When this equation is expressed in terms of the fraction of ants informed, denoted by $\hat{i}(t)$, we obtain the equation

$$\frac{d\hat{i}(t)}{dt} = n\lambda_0 \hat{i}(t)(1 - \hat{i}(t)), \tag{9}$$

from which we can see that speed of information spread increases linearly with the number of ants. The solution of this equation is presented in Appendix B, wherein it is also noted that the efficiency of the network at informing a particular ant in a given length of time satisfies the scaling property described in Appendix A.

Spatial Models

We here describe models that take into account the fact that ants do not hop randomly around the region but tend instead to remain in the same area. This has the consequence of reducing efficiency because of multiple searches of the same area (Cody 1971; Pyke 1978a; Dusenberry 1989). In addition, the speed at which information spreads through the colony is reduced because of the fact that informed ants will tend to be spatially clumped and thus more likely to encounter each other than uninformed ants. Since encounters between ants that are already informed have no effect on the spread of information, these encounters are "wasted," producing the reduced speed of information spread.

Spatial model of event discovery.—In this section we show how the shape of the ants' paths alters the efficiency of ants in discovering events because of self-intersection of the path. This self-intersection can be incorporated as a decrease in λ_0, because we are interested only in the new area searched by each ant on a time step. This modified λ takes into account two effects of turning
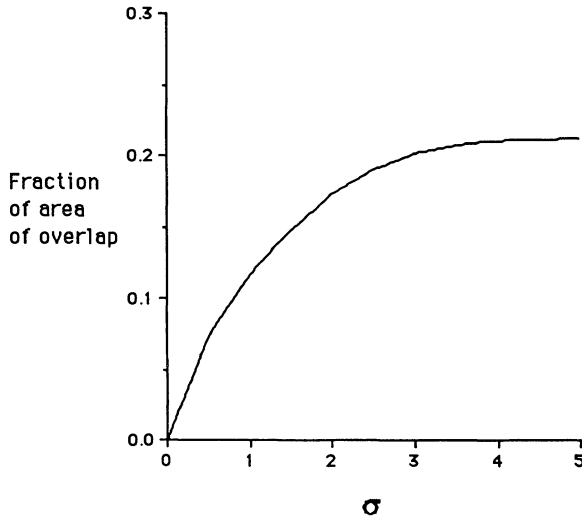
FIG. 2.—The expected fraction of the area searched by an ant on a given time step that is searched again on the subsequent step. Ants moving in straight lines ($\sigma = 0$) have no such overlap, whereas ants moving randomly have an expected overlap of ca. 20% of the area for standard values of the parameters.

angle: search of the same region on two consecutive steps due to a sharp turn and search of the same region after a delay of several steps.

The first effect, which proves to be fairly unimportant for the parameters we use, can be corrected for by finding the expected overlap of two consecutive steps as a function of σ. This can be done through a rather messy geometric calculation or through simulation. Figure 2 shows the calculated percentage of overlap as a function of σ over the reasonable range. Subtracting the area of overlap from the maximum territory explored, $2wr$, gives $\bar{a}$, the reduced area explored per step.

Estimating the extent of multiple searches of the same region after delays of more than a single time step requires computation of a diffusion coefficient for each ant. Kareiva and Shigesada (1983) give a formula for the diffusion coefficient associated with a correlated random walk, and this can be evaluated for the case of normally distributed turning angles to give the diffusion coefficient, D_σ, as a function of σ:

$$D_\sigma = \left(\frac{r^2}{4}\right) \frac{1 + e^{-\sigma^2/2}}{1 - e^{-\sigma^2/2}}. \tag{10}$$

The expected squared distance moved by an ant in k steps, M_k^2, is then given, for sufficiently large k, by

$$E(M_k^2) = 4D_\sigma k.$$

Decreased efficiency with high σ, and thus small D_σ, occurs because only a small region will be explored in k steps, making repeated investigations of the

same locations unavoidable. In particular, because the expected squared distance traveled by an ant in k steps is $4D_\sigma k$, search will remain concentrated inside a circle of area $4\pi D_\sigma k$. We take into account the directionality of the paths by assuming that search remains concentrated in a smaller circle of half the radius of the full circle centered halfway from the center to the edge, in the direction of the first step. The area of this smaller circle is $\pi D_\sigma k$. The fraction of this area actually explored by the ant can be approximated by pretending that the ant hops around randomly within this smaller region. The probability that a particular point is covered at least once is just the probability of success by at least one of k independent attempts, each of which has probability of success of $\tilde{a}/\pi D_\sigma k$, which is

$$1 - \left(1 - \frac{\tilde{a}}{\pi D_\sigma k}\right)^k \approx 1 - e^{-\tilde{a}/\pi D_\sigma}.$$

Therefore the total area explored is $\pi D_\sigma k(1 - e^{-\tilde{a}/\pi D_\sigma})$ and the fraction of the total area explored per step is

$$\tilde{\lambda} = \pi D_\sigma (1 - e^{-\tilde{a}/\pi D_\sigma})/\pi d_0^2. \tag{11}$$

Note that as $\sigma \to 0$ we have that $D_\sigma \to \infty$ and $\tilde{a} \to 2wr$, which can be shown to imply that $\tilde{\lambda} \to \lambda_0$ (see eq. [1]). Thus straight paths, which never intersect themselves, produce a maximally efficient search.

   Dusenbery (1989) summarizes a different approach, which focuses on computing expected times to capture of events. He considers only the case of a random walk without correlations, with diffusion coefficient D, and arrives at a result equivalent to

$$\tilde{\lambda} = \frac{2\pi D}{d_0^2} \frac{1}{\ln(d_0/w) - \frac{3}{4}}.$$

Note that this form, although qualitatively similar to equation (11), fails to have the correct limit as $D \to \infty$, because his method of approximation is appropriate only for uncorrelated random walks in large territories. The accuracy and range of applicability of these two methods of approximation warrant further investigation.

   We can substitute $\tilde{\lambda}$ for λ_0 in equation (4) to give $\hat{\psi}_n$, the corrected approximate fraction of events discovered, as a function of number of ants and event persistence as

$$\hat{\psi}_n = \frac{n\tilde{\lambda}}{p + n\tilde{\lambda}}. \tag{12}$$

   As in equation (5), we have that $\hat{\psi}_n$ satisfies the competitive scaling rule, or that

$$\hat{\psi}_n = \frac{n\hat{\psi}_1}{1 - \hat{\psi}_1 + n\hat{\psi}_1}.$$

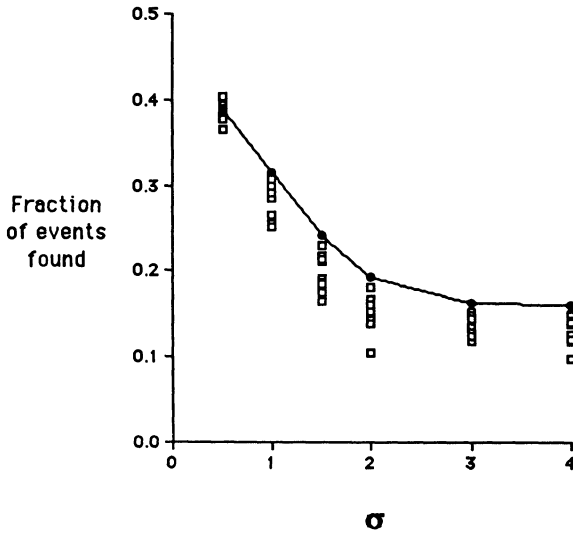Figure 3 compares $\hat{\psi}_n$ with the results of simulation over a range of σ.

FIG. 3.—Comparison of simulated fraction of events found by a single ant (*squares*) with the theoretical prediction $\hat{\psi}_n$ (*solid line*) given in eq. (12). Events here have long mean persistence times of 500 time steps ($\mu = 500$) to eliminate the bias created by evanescent events.

Spatial model of information spread.—We here present an approximation of the process of information spread through our network of ants. There is an extensive mathematical literature on the spread of epidemics, which are formally identical to the spread of information through direct contact. The method of approximation presented here differs from direct attack on partial differential equations (Diekmann 1978) or the contact process (Mollison 1977). Our method is designed to give estimates of the number and spatial distribution of ants informed throughout the dynamics.

Let $\tilde{I}$ represent the number of informed ants in this approximation, and $\tilde{S} = n - \tilde{I}$ represent the number of uninformed ("susceptible") ants. Let $\lambda_I \tilde{I}$ be the probability that an informed ant meets another informed ant during a particular time step, and $\lambda_{IS} \tilde{S}$ be the probability that an informed ant meets some uninformed ant during a particular time step. The variables λ_I and λ_{IS} will depend on the number and locations of the informed and uninformed ants and will vary with time. If the informed ants are clumped, we expect λ_I to be larger than $\bar{\lambda}$. Arguing as in *Null model of information spread*, we have

$$\frac{d\tilde{I}}{dt} = \lambda_{IS} \tilde{I} \tilde{S}, \tag{13}$$

which can be compared with equation (8).

The probability that an ant encounters another ant on a given time step is approximately $(n - 1)\bar{\lambda}$ because $\bar{\lambda}$ is the fraction of area explored by an ant on a given time step. This is not exact because both ants are moving, but it is a good approximation because the directions of movement of the two ants are

independent. Assuming that the average rate at which informed ants meet all other ants (i.e., the sum of the rates at which they meet informed ants and uninformed ants) is equal to the average rate at which any ant encounters other ants, we get

$$(n - 1)\bar{\lambda} = (\bar{I} - 1)\lambda_I + \tilde{S}\lambda_{IS}.$$

Solving for λ_{IS} and substituting into equation (13) gives

$$\frac{d\bar{I}}{dt} = \bar{I}[(n - 1)\bar{\lambda} - (\bar{I} - 1)\lambda_I].$$

Note that if $\lambda_I = \bar{\lambda}$ we reobtain equation (8) exactly.

To estimate λ_I, we define the "area" covered by the informed ants to be the mean square distance between pairs of informed ants and denote this by $A_I(t)$. The expected mean square distance between an arbitrary pair of ants is well approximated in practice by A_r, the mean square distance between two randomly chosen points in a disk of radius d_0 as long as the ants are roughly uniformly distributed throughout the region. It is not difficult to compute that $A_r = d_0^2$. We can then approximate the increased encounter rate of informed ants with other informed ants due to clumping by

$$\lambda_I = \bar{\lambda}\frac{A_r}{A_I}, \tag{14}$$

because encounter rates are inversely proportional to area covered.

We also need an equation describing the dynamics of A_I. The expected squared distance between two ants, like the squared distance moved by a single ant, increases linearly with time, but at a higher rate. Letting R_k denote the distance between two ants after k steps, we have

$$E(R_k^2) = (4D_\sigma + 4D_\infty)k. \tag{15}$$

The term $4D_\sigma k$ gives the expected squared distance moved by the first ant, and the term $4D_\infty k$, with diffusion coefficient equal to that of an uncorrelated random walk, gives the expected squared distance moved by the second ant relative to the first. The diffusion coefficient associated with the latter is that of an uncorrelated random walk because the paths of the two ants are uncorrelated with each other. We can then approximate A_I on time step k by

$$A_I = A_{I0} + (4D_\sigma + 4D_\infty)k,$$

where A_{I0} gives the initial area. Although this equation was derived for a fixed number of ants, it adequately models spatial spread when new ants are being informed, because newly informed ants are distributed more or less randomly with respect to all ants except the one that informed them and thus have mean squared distance from informed ants only slightly reduced from the average.

Because of the reflecting boundary, of course, the spread will not continue indefinitely, and we thus must put an upper bound of A_r on A_I. Substituting this into equation (8) gives the following pair of differential equations as an approxima-

tion for the spread of information and area informed:

$$\frac{d\tilde{I}}{dt} = \tilde{\lambda}\tilde{I}\left[(n - 1) - \frac{A_r}{A_I}(\tilde{I} - 1)\right]$$

and   (16)

$$\frac{dA_I}{dt} = \begin{cases} 4D_\sigma + 4D_\infty & \text{if } A_I < A_r \\ 0 & \text{otherwise}. \end{cases}$$

Appendix C gives the solution of this system of differential equations, demonstrating that the fraction of informed ants is approximately equal to the fraction of the total area informed.

This approach could be extended to model the spread of alarm through a network of ants, a process that differs from the spread of information only in that alarmed ants may alter their behavior as described by the parameters of r and σ.

RESULTS

The null models and spatial models make predictions about the efficiency of the network at discovering events and spreading information. We here give simulation results and compare them with the results of the theoretical models. All simulations were replicated 10 times, with fairly small variability among them.

We did not treat the reencounter avoidance parameter β analytically. However, as in the foraging model of Harkness and Maroudas (1985), this parameter turns out to have a negligible effect on the simulations, with simulations not only failing to show statistically significant differences between runs with $\beta = 0$ and $\beta = 1$, but failing to show differences at all. The reasons for this weak dependence on the avoidance parameter are unclear, but we presume it to be a consequence of the relative infrequency with which ants encounter each other. We have thus set β to be 0 (no avoidance) in the simulations discussed in the remainder of this article. The other parameter defaults are shown in table 1: we use $r = 1$, $w = 1.5$, $d_0 = 25$, $\mu = 50$, and $m = 10$ for the remainder of the article.

Event-Discovery Efficiency

In this section we illustrate three major results regarding event discovery: first, greater efficiency with more ants; second, lower efficiency with a higher turning angle; and third, reduction in cost of a high turning angle in large networks of ants. Simulation results are compared with three approximations. The first is the theoretically derived estimate of the fraction of events discovered, $\hat{\psi}_n$, and the second two are suitably calibrated versions of the random event disappearance rule, equation (5), and the constant event duration rule, equation (6). Calibration is achieved by setting the efficiencies of a single ant, $\hat{\phi}_1$ and ρ_1, to the efficiency measured in the simulations.

The first result, increased efficiency of larger colonies, is illustrated in figure 4 for a network of ants with a low σ of 0.5. Measured efficiency is very close to the scaling associated with the random event disappearance rule (eq. [5]) but is
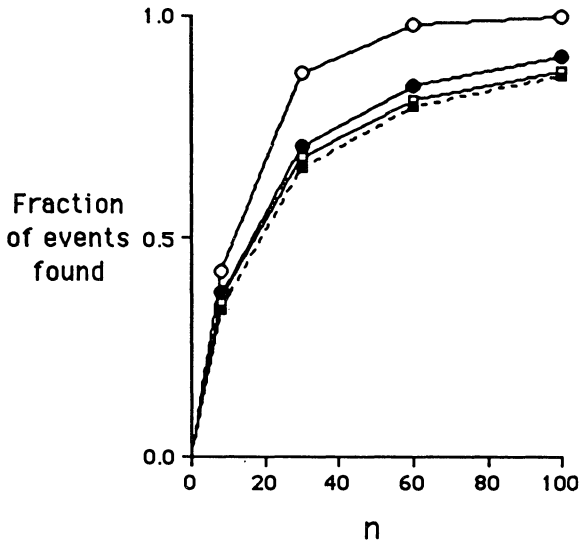
F1G. 4.—Efficiency as a function of network size for the low value of 0.5 for σ. Lines compare the mean of 10 simulations (*solid circles*), the theoretical approximation $\hat{\psi}_n$ (*solid squares, dotted line*), the results of the constant event disappearance rule (*open squares*), and the results of the constant event duration rule (*open circles*). In the last two, the success of a single ant is set equal to measured success.

much lower than the calibrated version of the constant event duration rule (eq. [6]) and is well approximated by $\hat{\psi}_n$. Note that the curve is concave down, indicating that, although total efficiency increases with more ants, the per-ant efficiency decreases with more ants, and that the colony fairly rapidly reaches the point of diminishing returns.

The second result, decreased efficiency with higher turning angle, is illustrated in figure 5 for networks of four different sizes. Note that each of the four curves decreases as σ increases, indicating diminished efficiency. Under our model of event production, high turning angle, which might seem to be a good idea because ants search a given area more thoroughly, always decreases efficiency. This result differs from that of Bovet (1981), who finds an intermediate optimum value of σ in a case with no territorial boundary and where individual searchers must return to the nest after each find, because of the trade-off between searching efficiently and remaining close to the nest. Simulations of foraging on a grid (Cody 1971; Pyke 1978a) have found an intermediate optimum level of turning in a square territory. Pyke (1978a) demonstrated that this is a consequence of the boundary effects, showing that nonreflecting boundaries and larger territories lead to a straighter optimal path, with a perfectly straight path being optimal in an infinite territory. Zimmerman (1979) found that random movement is optimal for organisms foraging on large patches that cannot be appreciably depleted in a single visit. Similarly, uncorrelated movement has no cost in systems where patches regenerate quickly (Cody 1971; Stillman and Sutherland 1990).

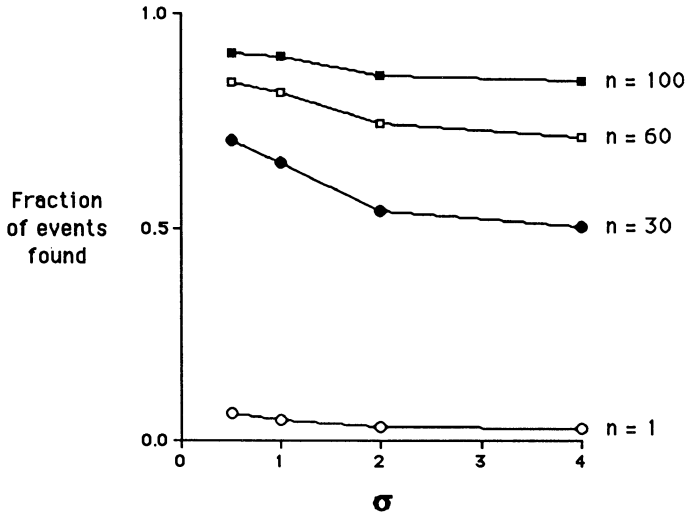A close examination of figure 5 indicates our third result, the reduced effect of

FIG. 5.—Simulated efficiency of networks of four different sizes for a range of values of σ. Note that efficiency alway decreases as σ increases, with the largest relative decrease occurring for small *n*.

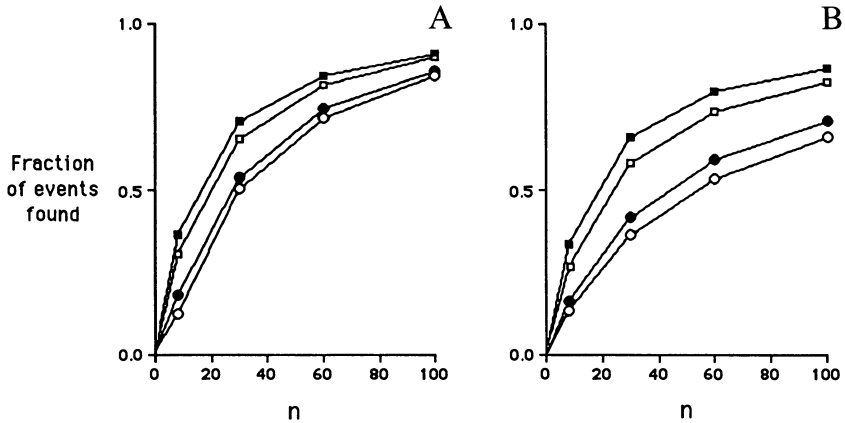FIG. 6.—*A,* The results of simulation of the event-discovery process for four values of σ as a function of *n: solid squares,* σ = 0.5; *open squares,* σ = 1; *solid circles,* σ = 2; and *open circles,* σ = 4. Note that the difference in efficiency caused by a higher turning angle decreases as *n* increases. *B,* The theoretical approximation for the same parameters fails to capture this phenomenon. See text for explanation of this discrepancy.

high turning angle on large networks. The result can be seen in this figure as a reduction, when *n* is large, in the relative difference between efficiency for high and low values of σ. Figure 6*A* illustrates this result in a different way by plotting the fraction of events found in simulations for various values of σ. Here, the diminished effect of a high turning angle on large networks shows up as conver- gence of the curves for large *n*. Figure 6*B*, which plots the theoretically predicted
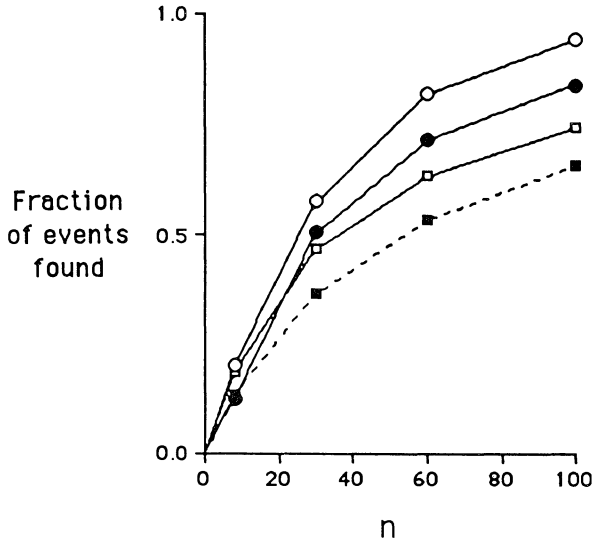
FIG. 7.—Efficiency as a function of network size for the high value of 4 for σ. The notation is the same as in fig. 4.

fraction of events discovered, $\hat{\psi}_n$, for the same values of σ, shows no such convergence for large n. The reason that a large turning angle produces a relatively smaller decrease in efficiency in large colonies than in small ones can be understood as follows. A large portion of the theoretically estimated decreased efficiency associated with high turning angle (see eq. [11]) is a consequence of multiple investigations of the same area several or many time steps apart. However, repeated investigations that take place many time steps apart will produce no reduced efficiency if the average residence time of events is short, because the information gathered on a previous visit rapidly becomes obsolete. Equation (7) shows that residence time of events decreases as the probability of discovery by ants increases, and we saw above that the probability of event discovery increases as the number of ants increase. Hence, as the number of ants increases, the effective self-interference of each ant decreases as a consequence of the shorter residence time of events. This is similar to the fact that an uncorrelated walk is close to optimal for organisms foraging in patches that quickly regenerate (Cody 1971; Stillman and Sutherland 1990).

How effective this process is can be seen in figure 7 (for $\sigma = 4$), which should be compared with figure 4 (for $\sigma = 0.5$). Both figures show how the fraction of events actually found in simulations compares with the theoretical prediction and with the random event disappearance and constant event duration rules. In figure 7, the fraction actually discovered lies almost exactly between the random event disappearance rule and the constant event duration rule when both n and σ are large, with the theoretical approximation, which ignores the effects of residence time, lagging behind. Large colonies can thus patrol efficiently even when individual patrollers follow apparently inefficient paths. Thus, if there are benefits to a
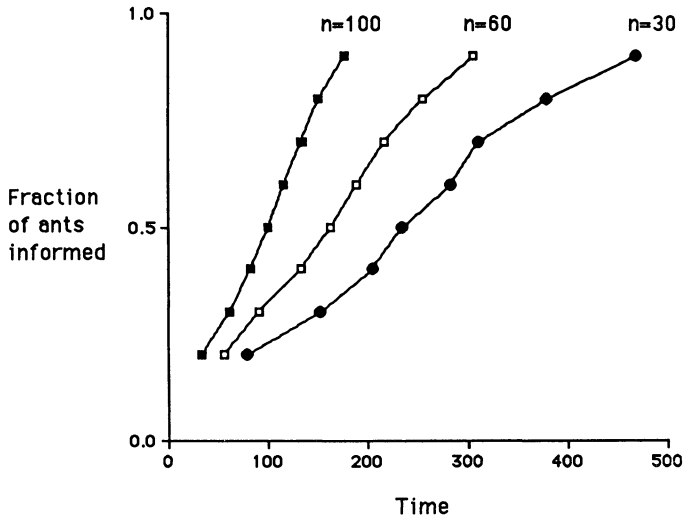
FIG. 8.—Trajectories showing the fraction of ants informed as a function of time for three network sizes. Note that large networks are more efficient than small networks.

large turning angle, such as the maintenance of information in the neighborhood where it was first gathered, large colonies need not sacrifice efficiency of event discovery to gain these other advantages.

Information Spread

The two basic effects noted for event discovery, increased efficiency with more ants and decreased efficiency for higher turning angle, also hold for efficiency of information spread. Here, efficiency is defined as the fraction of ants informed a certain amount of time after the first ant is informed. Figure 8 shows the fraction of ants informed as a function of time for various values of n for the low value 0.5 for σ.

Figure 9A shows the simulated fraction of ants informed as a function of time in a network of 100 patrollers for various values of σ and compares these with the solution of equations (16) to assess the quality of the approximation. The approximation captures qualitatively the significant effect high turning angle has in slowing down the process, here by as much as a factor of three. However, just as with event discovery, the approximation consistently overestimates the effect of large turning angle. Note that the fraction of ants informed increases approximately linearly rather than logistically as a function of time.

Figure 9B compares plots of the fraction of area informed as a function of time as found in simulations with the solution of the approximate equations (16), again giving fairly good agreement. Recall that the "area informed" is defined as the mean squared distance between informed ants and has a max:mum of d_0^2. The fraction informed is just the area informed divided by this maximum. Note that area informed increases linearly as a function of time. This implies that, if we plot the fraction of ants informed as a function of the area informed, the graph
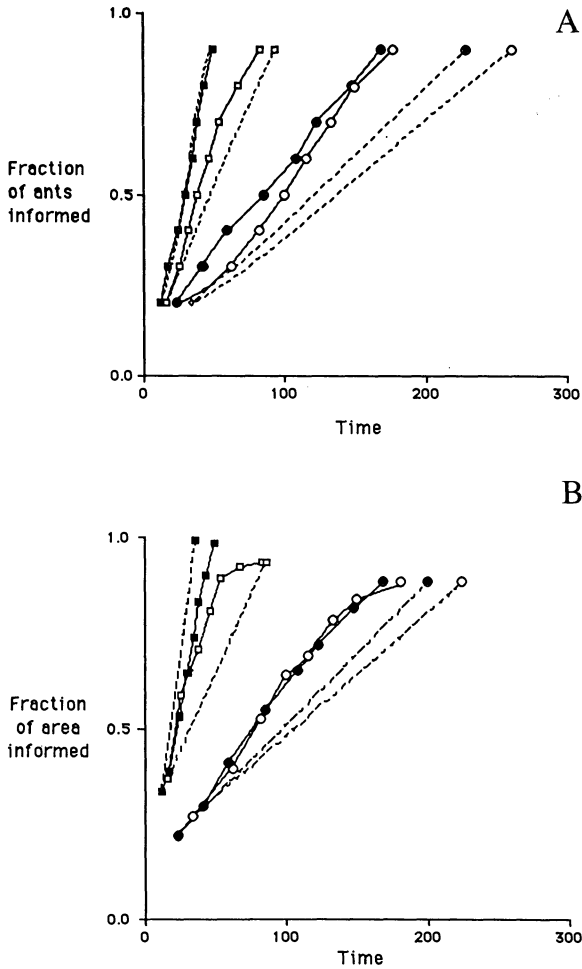
FIG. 9.—A, Trajectories of the fraction of ants informed; B, trajectories of the fraction of area informed as functions of time for a network of 100 ants and four values of σ: *solid squares*, σ = 0.5; *open squares*, σ = 1; *solid circles*, σ = 2; and *open circles*, σ = 4. *Solid lines* show the mean times from 10 simulations, and *dotted lines* show the results of eqq. (16) with initial conditions matched to those generated by simulations.

will again be close to linear, as shown in figure 10. In fact, it is shown in Appendix C that the fraction of area informed approximates the fraction of ants informed more or less independently of σ. This means that, when half the area is informed, roughly half the ants will be informed no matter what the value of σ is. The process of information spread then differs for different σ only insofar as the time until half the area is informed differs, with higher turning angle slowing the process down. Put another way, the process of information spread depends on σ only in rate and not in qualitative dynamics. Intuitively, it might seem that a higher turning angle would be effective in maintaining information near the loca-
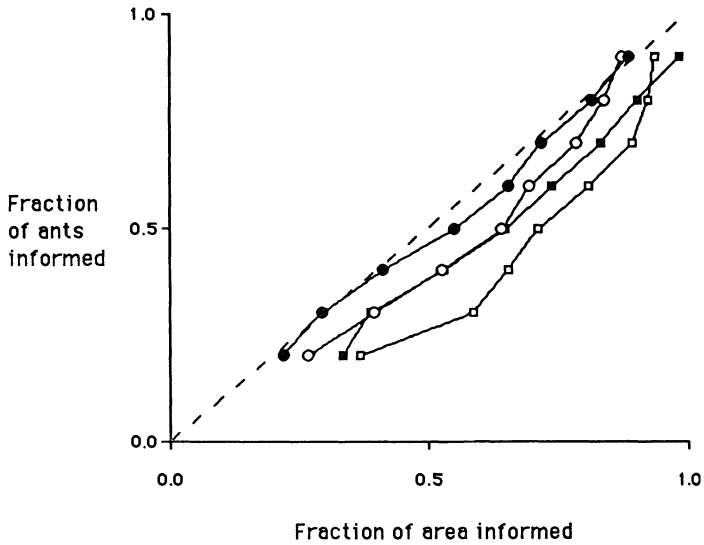
FIG. 10.—Trajectories plotting the fraction of ants informed against the fraction of area informed for a network of 100 ants and four values of σ. Symbols are the same as in fig. 9. The *dotted line* has slope 1, representing equality of the fraction of ants informed with the fraction of area informed. The trajectories begin in the lower left with a few ants informed in a small area and proceed upward to the right, nearly parallel to the *dotted line* (see App. C). Note that the large differences among curves for different values of σ have disappeared.

tion of its discovery and in informing all ants near that location. Our simulations show that this is not the case; a higher turning angle is not more effective in informing only those ants near the location where information was first discovered. Whether ants that alter behavior on being informed can achieve such information localization remains to be investigated.

DISCUSSION

This article provides a basic model of the potential consequences of information transfer through networks of patrolling ants, focusing on the efficiency with which such a network gathers and disseminates information. We give approximations of the efficiency of these processes that take into account their inherently spatial nature. The results lead to some general predictions. We first consider how efficiently an ant colony discovers events occurring randomly in space and disappearing randomly in time. We show that more ants find more such events, but that the efficiency of networks increases more slowly with network size than it would if events had constant duration. Path shape also influences the efficiency of a patrolling network. The rate at which events in the environment are discovered is diminished by a higher turning angle (more wiggly patrolling paths), because such paths increase the extent of multiple searches of given locations. We present an analytic approximation of this diminished efficiency, which takes into

account different degrees of directionality. Diminished efficiency proves to be less important in large networks because larger networks discover events more quickly and produce more rapid turnover, which reduces the cost of multiple searches of the same region.

Results for information spread are similar to those for event discovery. We show that the spread of information takes place more quickly in larger colonies and is impeded by increased turning angle. Although high turning angle slows information spread overall, it might seem intuitively likely that information spreads more efficiently locally, near the location of the discovery. Our simulations show that this is not the case. Instead, when some given fraction of ants has been informed, which takes longer with a higher turning angle, the number of informed ants near the discovered event is independent of the turning angle.

If future empirical observations indicate that the assumptions underlying this model are correct, our results regarding the effects of turning angle and number of ants on patrolling efficiency raise intriguing questions about the ecology of patrolling behavior. A first step will be to examine variation among colonies within species, to establish the extent to which both individual path shapes and colonywide patroller behavior are species specific. The next step will be to consider species differences in patrolling behavior. Constraints on patroller number are to some extent species specific, because overall colony size varies greatly among species. In addition, patroller number depends on environmental conditions, because colonies can produce more workers when food is abundant. The model predicts that patrollers will adopt straighter paths when patroller numbers are limited. This prediction invites interspecific comparisons. It could also be investigated intraspecifically, through experimental manipulation of food availability or of a colony's ability to produce patrollers. A recent study of *Lasius fuliginosus* shows that workers actively regulate the rate at which encounters occur, keeping contact rates high when numbers of workers per unit area are low, and avoiding contact when densities are high (Gordon et al. 1992). The spatial characteristics of this behavior remain to be investigated.

The model and method of analytical approximation presented here could be extended in several ways. The behavior of informed ants could be modified in step length (speed) and turning angle. For example, ants of many species increase both turning angle and velocity when alarmed. Changes in the behavior of informed ants could work either to keep information near the source or to disperse it rapidly throughout a larger region. The latter might serve to mobilize the entire colony rapidly about danger, while the former might be effective against a weak enemy or as a response to clumped food resources through a sort of area-restricted search. Preliminary simulations indicate that efficiency of patroller discovery of clumped events can be highly enhanced if patrollers increase turning angle in response to both event discovery and encounters with patrollers already exhibiting the higher turning angle.

The model could also be extended to include a measure of colony fitness. Such optimization models have been applied to various aspects of social insect behavior (Oster and Wilson 1978; Taylor 1978; Harkness and Maroudas 1985; Johnson

et al. 1987; Goss et al. 1989). To extend the present model in this way, it would be necessary to include details on the mode of forager recruitment and the size of food resources, as emphasized in Goss et al. (1989). In addition, the costs of failing to acquire or spread information must be put into the currency of colony fitness. Finally, the constraints on the number of ants available for the tasks of foraging and patrolling would need to be included, on the basis of the needs of the colony for ants to accomplish other tasks.

The combination of information retrieval and spread by groups of organisms makes this model suitable for general studies of group foraging. Several authors have considered the benefits of division of labor and the costs of interference associated with group foraging (Cody 1971; Levin et al. 1977; Pulliam and Caraco 1984; Clark and Mangel 1986), whereas others have looked at efficient means by which information can be spread through groups without centralized control (Brown 1988; Wilson and Hölldobler 1988; Seeley 1989). Our model gives a simple framework to attack these two problems simultaneously, although we ignore problems regarding conflicts of interest among individual ants, a problem important in group formation in other species (Pulliam and Caraco 1984; Clark and Mangel 1986). One possible test problem is consideration of how much more rapidly and accurately a communicating network can respond to changes in the environment than can an individual forager. Another such problem, mentioned above, is the consideration of the potential increased efficiency of networks in discovering and exploiting patchily distributed food through enhanced area-restricted search.

Our model features three innovations. First, we extend estimates of the efficiency of individual searchers to the efficiency of groups of patrollers, taking into account both group size and path characteristics. This model could be valuable for the study of a variety of group-living organisms (Pulliam and Caraco 1984). Second, we explicitly consider one mechanism of information spread through a network, focusing again on the effects of network size and individual movement characteristics. Our work is distinguished from earlier models (Beckers et al. 1990; Seeley et al. 1991) in that information exchange occurs throughout the foraging area rather than being concentrated at a single central location. The consideration of space in our model could contribute to work on information sharing in group-living organisms (Brown 1988). Finally, we develop analytic approximations of the processes of information collection and spread that take into account the effects of path characteristics on the efficiency of exploration and the effects of path characteristics and nonrandom distribution of informed individuals on the spread of information. In particular, our analysis of the process of information spread through the network requires approximation of the spatial logistic equation, which arises in the many applications that require modeling decentralized contact processes in continuous space. These approximations could be extended to model situations more general than those considered in this article and give sufficient quantitative detail for consideration of a wider range of parameters than would be possible through computer simulation alone. In addition to these theoretical innovations, our model raises new empirical questions about information transfer in encounters among patrollers.

APPENDIX A

Recall equation (3), the exact equation for the expected fraction of events discovered by n ants in the null model:

$$\phi_n = \frac{q_n}{p + q_n - pq_n},$$

where $q_n = 1 - (1 - \lambda_0)^n$. As with $\hat{\phi}_n$, we can find an expression for ϕ_n in terms of ϕ_1 to study the scaling of efficiency with network size. We have

$$\phi_1 = \frac{\lambda_0}{p + (1 - p)\lambda_0},$$

so that

$$\lambda_0 = \frac{p\phi_1}{1 - (1 - p)\phi_1}.$$

Substitution gives

$$\phi_n = \frac{1 - \left[\dfrac{1 - \phi_1}{1 - (1 - p)\phi_1}\right]^n}{1 - (1 - p)\left[\dfrac{1 - \phi_1}{1 - (1 - p)\phi_1}\right]^n}. \tag{A1}$$

It is interesting to note that as $p \to 1$ we obtain

$$\phi_n = 1 - (1 - \phi_1)^n,$$

which is the parallel efficiency of scaling familiar from Oster and Wilson (1978). Furthermore, as $p \to 0$ one obtains equation (5).

We now find a general expression that describes how ϕ_n scales as a function of n when the ants do not cooperate. Define $\phi(n, q)$ to be the efficiency of n ants when one ant has efficiency q. This should then satisfy

$$\phi(nm, q) = \phi(n, \phi(m, q)). \tag{A2}$$

This equation just says that one group of nm ants should be exactly as efficient as n groups of m ants. All functions mentioned in this appendix satisfy this scaling exactly.

Testing this equation requires the ability to modify q, the efficiency of a single ant. If

we know the values of $\phi(n, q_0)$ for all n for some q_0, we can then compute the value of $\phi(n, q)$ for any n and q predicted by equation (A2) as follows. For a given q, define $m(q)$ as the solution of

$$\phi(m(q), q_0) = q,$$

which will necessarily exist if efficiency ranges from zero to one as n runs from zero to infinity. Then

$$\phi(n, q) = \phi(n, \phi(m(q), q_0)) = \phi(nm(q), q_0),$$

which is known. In the absence of cooperation or interference, altering the efficiency of a single ant has the effect of scaling the horizontal axis. If we increase q_0 to q and observe that

$$\phi(n, q) > \phi(nm(q), q_0),$$

it seems that the larger group of ants does worse than it should, indicating interference. If on the other hand we observe that

$$\phi(n, q) < \phi(nm(q), q_0),$$

it would seem that the larger group of ants does better than it should and is cooperating.

Note that the direction of the inequality, and thus the deduction of cooperation or interference, might depend on the mechanism by which the efficiency of a single ant is modified. For example, in our model, modifying the efficiency of a single ant by changing its turning angle indicates cooperation, whereas modifying efficiency by changing its perceptual radius indicates neither cooperation nor interference.

APPENDIX B

We here present the solution of equation (9) and consider whether these solutions appear cooperative in the sense of Appendix A. Recall equation (9):

$$\frac{d\hat{i}}{dt} = n\lambda_0 \hat{i}(t)(1 - \hat{i}(t)),$$

with the initial conditions that a fraction i_0 ants is informed at time 0. Setting

$$c_0 = \frac{i_0}{1 - i_0},$$

we have

$$\hat{i}(t) = \frac{c_0 e^{n\lambda_d t}}{1 + c_0 e^{n\lambda_d t}}. \tag{B1}$$

If we fix a particular time T, we can think of $i(T)$ as the efficiency of the network informing a particular ant. Letting ϕ_1 be $i(T)$ for $n = 1$, we have

$$\phi_1 = \frac{c_0 e^{\lambda_d T}}{1 + c_0 e^{\lambda_d T}}.$$

We can then compute that

$$\phi_n = \frac{\phi_1^n}{\phi_1^n + (1 - \phi_1)^n},$$

which can be easily shown to satisfy equation (A2). Thus, although a larger network informs a larger fraction of the ants in a given interval of time, it does not do so in a way that shows cooperation among groups.

APPENDIX C

This appendix gives the solution of equations (16), which approximate the spread of information in space:

$$\frac{d\bar{I}}{dt} = \tilde{\lambda}\bar{I}\left[(n-1) - \frac{A_r}{A_I}(\bar{I}-1)\right]$$

and

$$\frac{dA_I}{dt} = \begin{cases} 4D_\sigma + 4D_\infty & \text{if } A_I < A_r \\ 0 & \text{otherwise.} \end{cases}$$

The method is to scale variables to produce a single equation of simpler form and show how the solution of the simplified equation depends on the single remaining parameter.

First, we define the variables for the fraction of ants informed and the fraction of area informed, respectively, by defining

$$x = \frac{\bar{I}-1}{n-1}$$

and

$$a = \frac{A_I}{A_r}.$$

We assume that n is sufficiently large that x can be approximated by $\bar{i}/n$. Because area changes linearly with time, we can use a as the independent variable and arrive at the equation

$$\frac{dx}{da} = \gamma x\left(1 - \frac{x}{a}\right), \tag{C1}$$

where the single parameter γ is given by

$$\gamma = \frac{\tilde{\lambda}A_r n}{4D_\sigma + 4D_\infty}. \tag{C2}$$

By setting

$$\tau = \gamma a$$

and

$$y = \gamma x,$$

we can rewrite equation (C1) as

$$\frac{dy}{d\tau} = y\left(1 - \frac{y}{\tau}\right). \tag{C3}$$

This equation makes no reference to any of the parameters, indicating the independence of this process from parameters in everything but rate.

Note from equation (C2) that γ will be of order n as long as the diffusion coefficient is not too large. We assume from now on that γ is large, which is equivalent to assuming a large network of ants that can be reasonably thought of as diffusing. Recalling that a is the fraction of area covered and hence runs from some positive initial value of order $1/n$ up to 1, we have that τ runs from an initial value τ_0 of order 1 up to the large value of γ. Equation (C3) can be solved exactly by changing variables to $u = 1/y$, giving the solution

$$y(\tau) = \frac{e^\tau}{e^{\tau_0}/y_0 + \int_{\tau_0}^\tau (e^t/t)\,dt}, \tag{C4}$$

where y_0 is the value of y when $\tau = \tau_0$. When τ is fairly large, as it will be when it approaches its limit of γ, the integral in the denominator can be expanded asymptotically (Bender and Orszag 1978) as

$$\int_{\tau_0}^{\tau} \frac{e^t}{t} \, dt \approx \frac{e^{\tau}}{\tau} + \frac{e^{\tau}}{\tau^2}.$$

Substituting this into equation (C4) gives

$$y \approx \frac{\tau}{1 + 1/\tau}$$

or

$$x \approx a - \frac{1}{\gamma}.$$

The fraction of ants informed thus comes to approximate the area informed independently of the parameters, as shown in figure 10. The increased efficiency of larger networks illustrated in figure 8 holds only for small networks, for which the assumption of large γ is not valid. For larger n, the solution is nearly independent of n, because of the fact that diffusion, not encounter rate, limits the spread of information under these assumptions.

LITERATURE CITED

Bailey, N. T. J. 1975. The mathematical theory of infectious diseases and its applications. Griffin, London.
Beckers, R., J. L. Deneubourg, S. Goss, and J. M. Pasteels. 1990. Collective decision making through food recruitment. Insectes Sociaux 37:258–267.
Bender, C. M., and S. A. Orszag. 1978. Advanced mathematical methods for scientists and engineers. McGraw-Hill, New York.
Bossert, W. H., and E. O. Wilson. 1963. The analysis of olfactory communication among animals. Journal of Theoretical Biology 5:433–469.
Bovet, P. 1981. Optimal randomness in foraging movement: a central place model. Pages 295–302 in M. Cosnard, J. Demongeot, and A. Le Breton, eds. Rhythms in biology and other fields of application. Lecture Notes in Biomathematics. Vol. 49. Springer, Berlin.
Bovet, P., and S. Benhamou. 1988. Spatial analysis of animals' movements using a correlated random walk model. Journal of Theoretical Biology 131:419–433.
Brown, C. R. 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. Ecology 69:602–613.
Camazine, S., J. Sneyd, M. J. Jenkins, and J. D. Murray. 1990. A mathematical model of self-organized pattern formation in the combs of honeybee colonies. Journal of Theoretical Biology 147:533–571.
Clark, C. W., and M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45–75.
Cody, M. L. 1971. Finch flocks in the Mohave Desert. Theoretical Population Biology 2:142–158.
Deneubourg, J. L., S. Goss, N. Franks, and J. M. Pasteels. 1989. The blind leading the blind: modeling chemically mediated army ant raid patterns. Journal of Insect Behavior 2:719–725.
Diekmann, O. 1978. Thresholds and travelling waves for the geographical spread of infection. Journal of Mathematical Biology 6:109–130.
Dusenberry, D. B. 1989. Ranging strategies. Journal of Theoretical Biology 136:309–316.
Frehland, E., B. Kleutsch, and H. Markl. 1985. Modelling a two-dimensional alarm process. Biosystems 18:197–208.
Gordon, D. M. 1983. The relation recruitment rate to activity rhythms in the harvester ant, *Pogonomyrmex barbatus*. Journal of the Kansas Entomological Society 56:277–285.

———. 1987. Group-level dynamics in harvester ants: young colonies and the role of patrolling. Animal Behaviour 35:833–843.

———. 1988. Group-level exploration tactics in fire ants. Behaviour 104:162–175.

———. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. American Naturalist 138:379–411.

Gordon, D. M., R. E. Paul, and K. Thorpe. 1992. What is the function of encounter patterns in ant colonies? Animal Behaviour (in press).

Goss, S., and J. L. Deneubourg. 1989. The self-organizing clock pattern of *Messor pergandei* (Formicidae, Myrmicinae). Insectes Sociaux 36:339–346.

Goss, S., J. L. Deneubourg, J. M. Pasteels, and G. Josens. 1989. A model of noncooperative foraging in social insects. American Naturalist 134:273–287.

Harkness, R. D., and N. G. Maroudas. 1985. Central place foraging by an ant (*Cataglyphis bicolor* Fab.): a model of searching. Animal Behaviour 33:916–928.

Hoffman, G. 1983. The random elements in the systematic search behavior of the desert isopod *Hemilepistus reaumuri*. Behavioral Ecology and Sociobiology 13:81–92.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap, Cambridge, Mass.

Johnson, L. K., S. P. Hubbell, and D. H. Feener, Jr. 1987. Defense of food supply by eusocial colonies. American Zoologist 27:347–358.

Jutsun, A. R. 1979. Interspecific aggression in leaf-cutting ants. Animal Behaviour 27:833–838.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia (Berlin) 56:234–238.

Lenoir, A., and P. Jaisson. 1982. Evolution et rôle des communications antennaires chez les insectes sociaux. Pages 157–180 *in* P. Jaisson, ed. Social insects in the tropics. Vol. 1. Université Paris-Nord, Paris.

Leonard, J. G., and J. M. Herbers. 1986. Foraging tempo in two woodland ant species. Animal Behaviour 34:1172–1181.

Levin, S. A., J. E. Levin, and R. T. Paine. 1977. Snowy owl predation on short-eared owls. Condor 79:395.

Mollison, D. 1977. Spatial contact models for ecological and epidemic spread. Journal of the Royal Statistical Society 39B:283–326.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in the social insects. Monographs in Population Biology, no. 12. Princeton University Press, Princeton, N.J.

Pasteels, J. M., J. L. Deneubourg, and S. Goss. 1987. Self-organizing mechanisms in ant societies. I. Trail recruitment to newly discovered food sources. Pages 155–175 *in* J. M. Pasteels and J. L. Deneubourg, eds. From individual to collective behavior in social insects. Experientia Supplementum. Vol. 54. Birkhauser, Basel.

Porter, S. D., and C. D. Jorgensen. 1981. Foragers of the harvester ant, *Pogonomyrmex owyhei:* a disposable caste? Behavioral Ecology and Sociobiology 9:247–256.

Pulliam, H. R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 122–147 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford.

Pyke, G. H. 1978a. Are animals efficient harvesters? Animal Behaviour 26:241–250.

———. 1978b. Optimal foraging: movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13:72–98.

Seeley, T. D. 1989. Social foraging in honeybees: how nectar foragers assess their colony's nutritional status. Behavioral Ecology and Sociobiology 24:181–199.

Seeley, T. D., S. Camazine, and J. Sneyd. 1991. Collective decision-making in honeybees: how colonies choose among nectar sources. Behavioral Ecology and Sociobiology 28:277–296.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

Stillman, R. A., and W. J. Sutherland. 1990. The optimal search path in a patchy environment. Journal of Theoretical Biology 145:177–182.

Taylor, F. 1978. Foraging behavior of ants: theoretical considerations. Journal of Theoretical Biology 71:541–563.

Wehner, R. 1987. Spatial organization of foraging behavior in individually searching desert ants *Cataglyphis* (Sahara Desert) and *Ocymyrmexis* (Namib Desert). Pages 15–42 *in* J. M. Pasteels and J. L. Deneubourg, eds. From individual to collective behavior in social insects. Experientia Supplementum. Vol. 54. Birkhauser, Basel.

Wilson, E. O., and B. Hölldobler. 1988. Dense heterarchies and mass communication as the basis of organization in ant colonies. Trends in Ecology & Evolution 3:65–68.

Zimmerman, M. 1979. Optimal foraging: a case for random movement. Oecologia (Berlin) 43:261–267.

Associate Editor: Geoffrey A. Parker