

Active Random Walkers Simulate Trunk Trail Formation by Ants

Frank Schweitzer^{a,b}, Kenneth Lao^b, Fereydoon Family^b

^a *Institute of Physics, Humboldt University, Unter den Linden 6, 10099 Berlin, Germany, e-mail: frank@physik.hu-berlin.de*

^b *Emory University, Department of Physics, Atlanta, GA 30322, U.S.A.*

Abstract

A simple model for interactive structure formation is studied to simulate the trail formation by ants based on local chemical communication. In our model, active random walkers, which do not have the ability of visual navigation or storage of information, first have to discover different distributions of food sources and then have to link these sources to a central place by forming a trail, using no other guidance than the chemical markings produced by themselves. The simulations show the spontaneous emergence of a collective trail system due to self-organization, which is both stable and flexible to include newly discovered sources. The typical dendritic foraging patterns of desert ants, reported by Hölldobler and Möglich (1980), are reproduced by the simulations.

Key words: trail formation, foraging patterns, self-organizing systems

1 Introduction

Searching and homing strategies of small-brain animals, like ants, have been developed to such an high level, that one may attribute terms like “intelligence” (Pricer, 1908) or “mental capacity” (Wilson, 1971) to this kind of behavior. Desert ants for example find their way back to the nest, after their foraging excursions have led them more than 250 m away from the start (Wehner, 1987). This impressive performance may depend on several capabilities cooperating, such as

- (i) geocentric navigation, which uses landmarks (for desert ants, genus *Cataglyphis* cf. Wehner and Rüber, 1979, with respect to cognitive maps see also Wehner and Menzel, 1990)

- (ii) egocentric navigation, which is based on route integration (dead reckoning) and provides the animal with an continuously up-dated homeward based vector (cf. Müller and Wehner, 1988, Wehner and Wehner, 1990, for desert ants, genus *Cataglyphis*)

Both mechanisms are based on visual navigation and on the capability of internal storage of information (memory). On the other hand, different ant species are also capable of external storage of information, e.g. by setting chemical signposts (pheromones), which provide additional olfactory orientation. These chemicals are not only used for orientation, but also for communication between the individuals in a rather complex way (cf. for instance the review about chemical communication in ants by Hölldobler and Wilson, 1990). External storage of information by means of chemicals plays an important role in establishing the impressive trail systems, group-raiding ant species are known for. These trails provide the basic orientation for foraging and homing of the animals. A more detailed description of this phenomenon is given in Sect. 2.

In our paper we want to discuss the problem whether these trail patterns could be also obtained under the restrictions, that (i) no visual navigation and internal storage of information is provided, (ii) in the beginning, no chemical signposts exist which lead the animals to the food sources and afterwards back to the nest.

Certainly, these restrictions do not describe the situation of ants which can use different levels of orientation mentioned, and in this sense are rather complex creatures (cf. also Haefner and Crist, 1994, Crist and Haefner, 1994, who investigated the influence of memory and space perception on foraging ants, *Pogonomyrmex*). Our approach starts from a quite different perspective. We do not try to reveal the biological constitutions of ants for solving this problem, but propose a simple model to reproduce the characteristic trail patterns observed in ants by means of Active Random Walkers which have far less complex capabilities than the biological creatures. Our model therefore may serve as a toy model to test what kind of interaction between individuals may lead to a trail system and what are the minimal conditions for its existence.

Active Walker models have been previously used within a physical framework to describe different kinds of pattern formation (cf. Lam and Pochy, 1993, Schweitzer and Schimansky-Geier, 1994, Lam, 1995, Schimansky-Geier *et al.*, 1996). By modeling microscopic local interactions between the walkers and their environment, the emergence of a variety of macroscopic structures could be obtained which are not readily predictable from the basic equations.

Here the Active Walker model is used to simulate the formation of directed trails, as observed in group-raiding ants. In our model, the formation of trail patterns is solely based on simple local chemical communication between the walkers, with no additional capabilities of orientation. We will show that the spontaneous emergence of a collective trail system can be described as a self-organizing process.

2 Biological Observations of Trunk Trail Formation in Ants

The behavioral observations of trunk trail formation in ants are concluded in a most succinct manner by Hölldobler and Wilson (1990). As pointed out on page 285 of their comprehensive treatise *The Ants*, “a great many species in the *Myrmicinae*, *Dolichoderinae*, and *Formicinae* lay trunk trails, which are traces of orientation pheromones enduring for periods of days or longer. In the case of leafcutter ants of the genus *Atta*, harvesting ants of the genus *Pogonomyrmex*, the European shining black ant *Lasius fuliginosus*, and the polydomous wood and mound-building ants in the *Formica exsecta* and *rufa* groups, the trails can last for months at a time (...) Trunk trails used for foraging are typically dendritic in form. Each one starts from the nest vicinity as a single thick pathway that splits first into branches and then into twigs (see Fig. 1). This pattern deploys large numbers of workers rapidly into foraging areas. In the species of *Atta* and the remarkable desert seed-eating *Pheidole militicida*, tens of even hundreds of thousands of workers move back and forth on a daily base. A few workers drift away from the main trunk route, but most do not disperse on a solitary basis until they reach the terminal twigs. When small food items are encountered, the workers carry them back into the outer branches of the system and then homeward. The twigs and branches can now be envisioned as tributaries of ant masses flowing back to the nest. When rich deposits of food are found, on the other hand, the foragers lay recruitment trails to them. In time new deposits of orientation pheromone accumulate along which foragers move with the further inducement of recruitment pheromones. By this process the outer reaches of the trunk-trail system shift subtly from day to day.”

We note, that the foraging behavior described above, is, to a certain extent, different from that of the army ants (e.g. *Eciton burchelli* and other species of *Eciton* and *Dorylus*), although the foraging patterns of different *Eciton* species also show a dendritic structure (cf. Sudd and Franks, 1987, or Hölldobler and Wilson, 1990). But *Eciton burchelli* is a swarm raider, where the foraging workers spread out into a fan-shaped swarm with a broad front, whereas most other army ant species are column raiders, where the mass moves outwards along narrow trails (cf. the pioneering works of Scheirla, 1933 and 1940; and Rettenmeyer, 1963). Recently, Deneubourg *et al.* (1989), (see also Franks *et al.*, 1991) have presented a computer simulation model showing how these patterns could be generated from the interactions between identical foragers. This model is based on a trail-laying and trail following behavior with an adjustable speed of the ants. It counts on a single pheromone and does not include additional recruitment.

The phenomena, discussed in this paper, are based on two different stages, (i) exploration of the food sources by solitary scouts, and (ii) recruitment and exploitation of the food sources. As reported e.g. for the case of the tropical ponerine ant, *Leptogenys ocellifera*, (Maschwitz and Mühlenberg, 1975, cf. also the review by Wehner, 1992) during the first stage, individual “scout” ants search solitarily for arthropod prey. On their way out from the nest, they deposit a trail pheromone consisting of poison-gland secretions, providing orientational cues. Once successful, the scout, on its way back to the nest, lays a pheromone trail consisting of both poison-gland and pygidial-gland secretions, where the latter stimulate recruitment (Attygalle *et al.*, 1988, 1991). Along this recruitment trail up to 200 nest mates will move in a single file, one behind the other (and not in a swarm raid) from the nest to the newly discovered food source and transport it to the nest.

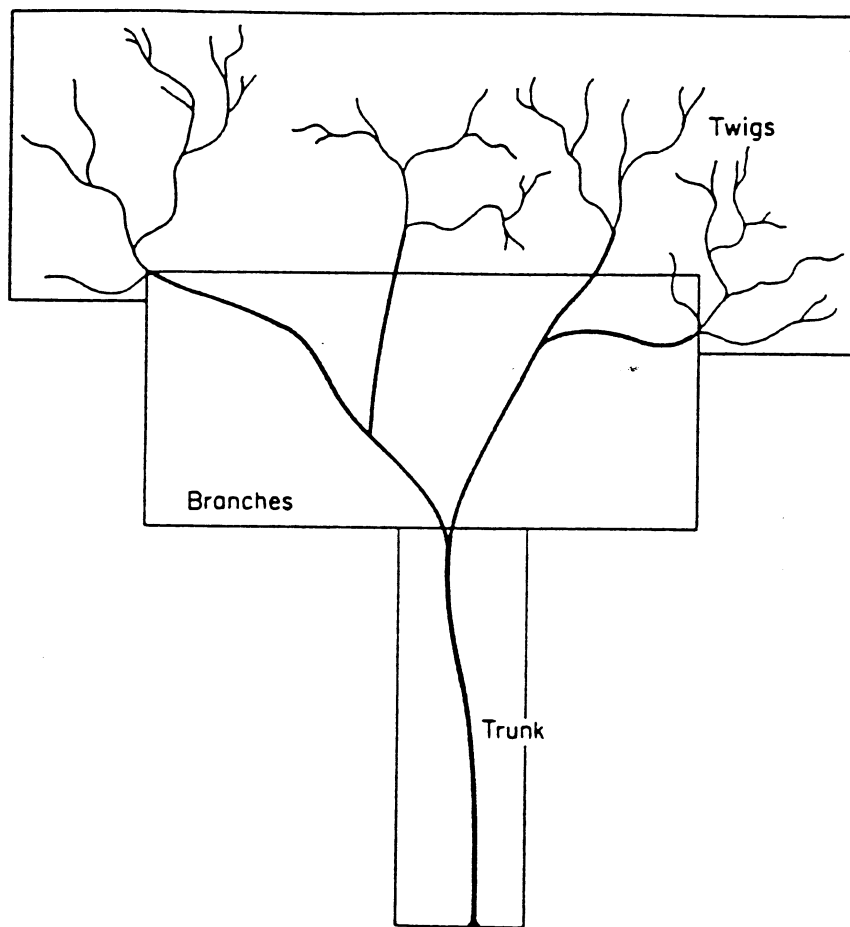


Figure 1: Schematic representation of the complete foraging route of *Pheidole milicida*, a harvesting ant of the southwestern U.S. deserts. Each day tens of thousands of workers move out to the dendritic trail system, disperse singly, and forage for food. (From Hölldobler and Möglich (1980); reprinted in Hölldobler and Wilson (1990), p. 285)

As pointed out, trunk trails are used to bring a large number of foragers in a most effective way into the foraging area and to recruit new nest mates to the new food. The trails are used with a considerable fidelity both for the foraging and the return trips. But trunk trails are also used as connecting routes by ants that occupy multiple nests, as reported for the case of *Crematogaster* and species in the dolichoderine genera *Azteca*, *Hypoclinea*, and *Iridomyrex* (Hölldobler and Wilson, 1990)

3 Basic Assumptions of the Active Walker Model

In order to simulate the trunk trail formation in ants, as described in the previous section, we start with an outline of our model. Here the basic elements are Active Walkers, which move on a surface. The term “active” means that the walkers are able to interact with the surface and thus change the state of the surface, which in turn influences their further motion.

In order to specify the motion and the action of a walker, we assume the following:

- (i) The walker performs a biased random walk, which means it moves in discrete steps with different probabilities for the different directions of the next step. The bias of the walk reflects a tendency to go forward and to persist to a certain degree into the direction the walker already has, instead of steadily changing this direction like a simple random walker. The biased random walk should be an appropriate assumption in the case of ants which have an oblonged body with a bilateral symmetry and, therefore, do not move like pure random walkers. We note, that random walk theory - besides its physical applications (cf. e.g. Family and Gould, 1984) - has been turned out to be a very useful tool for describing also biological motion (Fürth, 1920, Alt, 1980; Berg, 1983; Alt and Hoffmann, 1990).
- (ii) The walker is able to produce a chemical, which, in the case of ants, is known as pheromone. It is assumed that a walker during its walk continuously drops the chemical (sets markings) and thus changes the state of the surface locally. The chemical decomposes in time due to an external dynamics, decreasing the local concentration. That means, only those markings will survive which are steadily renewed by the walkers.
- (iii) The walker is able to recognize the chemical, if it is in the close vicinity of its site - which means a short-range or local recognition rather than a “view” over a long distance. It is known that insects like ants are able to measure concentration gradients of pheromones (cf. Payne *et al.*, 1986; Calenbuhr and Deneubourg, 1990; Edelstein-Keshet, 1994) - but only in a certain range of space, determined by the length and the angle between their antennae and if the concentration locally exceed a certain threshold. We count on that fact by considering a broken symmetry of the walker, it can check for a gradient of the chemical only in a certain range of space. Different from a simple physical particle, that feels a gradient from every direction, the walker feels a gradient locally and only within a certain angle around the direction of its motion. The threshold parameter is assumed to be a small parameter, indicating that the walker is able to detect even small amounts of chemical.
- (iv) The non-linear feedback between the motion of the walker and the changing surface state is given by the fact, that the walker can change the direction of its motion towards the highest local concentration of the chemical detected. This kind of response to chemical gradients is known from biology as *chemotaxis* and modifies the biased random walk (Alt, 1980). Since the walkers are the ones producing the chemicals which in turn influences their motion, a recursive interaction occurs, which results in an indirect local interaction between the walkers.

In more general terms, the active walkers represent individuals (agents) existing in an environment, which can be changed by them, but also feeds back to their behavior. So far, there exist some analogies to Artificial Agents Systems, discussed in the AL community (cf. Meyer and Wilson, 1991; Maes, 1992; Langton, 1994), but we have to note some differences. In our model, the active walkers are treated more or less as physical particles, which have no memory and, therefore, cannot perform meaningful actions. In particular, the walkers do *not* interact *directly* with each other, further they do not learn from their actions and don't have a free will to choose among different options. They rather behave in an automatic way, responding to physical forces like gradients or inertia - which gives us the possibility to treat these models also analytically within a physical framework (Kayser *et al.*, 1992; Schweitzer and Schimansky-Geier, 1994).

4 Self-Consistent Track Formation with Active Walkers

The model introduced simulates a chemotactic response to a chemical gradient which has been produced by the walkers themselves. This non-linear feedback should be one of the basic ingredients for trail following in ants. Here it is assumed that the ants continuously mark their way with a pheromone. Different species, as the army ants *Eciton* or the Argentine ant *Iridomyrmex humilis* behave that way. Therefore, chemical signposts are always present, and a decision which trail to follow depends only on the actual pheromone concentration (Goss *et al.*, 1989; Calenbuhr and Deneubourg, 1990).

With respect to biology, there are different parameters which may influence the occurrence of trail patterns, such as trail fidelity, traffic density, sensitivity and detection distance, endurance of the trail etc. (cf. Haefner and Crist, 1994, Edelstein-Keshet *et al.*, 1995). Since our model considers only minimal assumptions for the trail formation, the generated trails should be simply described by a space and time dependent chemical field $c(r, t)$ which obeys the following reaction equation:

$$\frac{dc(r, t)}{dt} = -\gamma c + Q(r, t), \quad Q(r, t) = \sum_{i=1}^N q^0 \delta(r - r_i(t)) \quad (1)$$

The term $-\gamma c$ describes the decomposition of the chemical, γ being the decomposition rate, whereas the term $Q(r, t)$ describes the local production of the chemical. q^0 is the rate at which the walker i drops the chemical per step at position r_i . $\delta(r - r_i(t))$ is the delta function, which is 1 for $r = r_i$ and zero otherwise.

The Active Random Walkers respond to the chemical field as described in Sect. 3, however they do not act in a deterministic way, but only with a certain probability because due to the thermal noise, fluctuations always occur in the system. One typical trail pattern which results from the model is shown in Fig. 2 by means of computer simulations.

The main conclusion which can be drawn from Fig. 2 is the transition of the initial random movement of the walker population into a movement along distinct trails which are used with different frequencies. Fig. 2 indicates that large areas of the simulated surface are left empty, since the

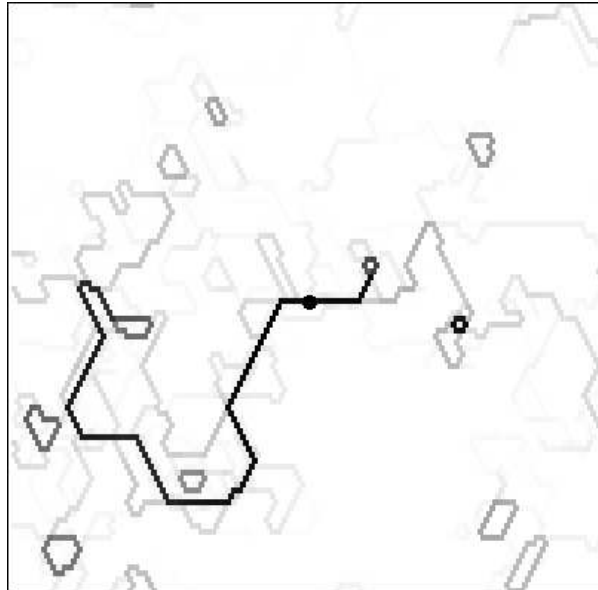


Figure 2: Trail system generated by $N = 100$ Active Random Walkers after 5.000 simulation steps. In the beginning, the walkers have been released at once in the middle (nest) of the triangular lattice (size 100×100). The grey scale of the trails encodes the frequency of use. Parameters: $\gamma = 0.005$, $q^0 = 80$ (arbitrary units)

walker community is bound to the existing trails. The trail pattern remains as a quasi-stationary structure: The main trails, indicated by a deeper grey, form a stable structure, only minor trails occur or disappear from time to time due to the probabilistic effects included into the model.

Trail patterns like Fig. 2 have been also obtained by computer simulations of Edelman-Keshet (1994, 1995), who investigated the influence of individual properties of ants in trail following on the resulting pattern. Moreover, similar trail patterns have been discussed in the context of gliding myxobacteria which produce slime tracks commonly used for movement and aggregation (Stevens, 1990, Stevens and Schweitzer, 1996).

However, for the formation of trunk trails as described in Sect. 2, the model introduced so far does not seem to be sufficient enough, since there are no destination points, such as food sources present. Hence, the simulated trails in Fig. 2 are *undirected* tracks used for movement and in this sense are different from a *directed trail* which is a specific link between a source and a destination.

In order to simulate foraging trails in ants, the most simple assumption could be that *only* individuals which found food create a pheromone trail, while turning straight back to the nest. These trails can be used by other ants to find the food sources, once they found the trails. These simulations have to overcome the problem where the first ant which found food got the information from to find its way back home. In biological systems, geocentric or egocentric navigation as described in Sect. 1, could provide this additional information needed for successfully returning to the nest.

Since our model simulates the formation of trunk trails without counting on navigation and internal storage of information, our main assumption is that a simple chemotactic response would be sufficient to generate trails between the nest and the food sources. Indeed, Fig. 2 shows that chemotaxis is able to produce trail patterns. However, we have to distinguish trails which have been created during the (unsuccessful) search for food from trails which really lead to a food source. In our model, this additional information is encoded by assuming that the walkers now produce and respond to two chemical fields, as will be described below.

5 Assumptions for Directed Trail Formation with Active Walkers

Different from the arbitrary *non-directed* track patterns, *directed trails* should link a starting point (e.g. a nest) to a destination point (e.g. a food source). In order to define start and destination, we assume on the two-dimensional surface a center (nest) where the walkers are initially concentrated, and a number of food sources unknown to the walkers. Both, the nest and the food sources, *do not attract* the walkers by a certain long-range attraction potential, they are just particular sites of a certain size (defined in lattice sites afterwards).

In addition to the features of the walker described in Sect. 3, we now introduce some specific assumptions of the model, in order to simulate the formation of trunk trails in close relation to the biological observations described in Sect. 2.

- (i) The walkers are now able to produce two kind of chemicals (or pheromones), A and B. As reported in Sect. 2, ants can surely use different kind of pheromones for orientation and recruitment, where the orientation pheromones comprising the trunk trails are often secreted by glands different from those that produce the recruitment pheromones. Which kind of chemical is used by a walker, will be specified depending on whether it has found food or not. In this model it is assumed further that, as a question of disposal, the quantity of chemical produced by a specific walker after leaving the nest or the food source, decreases exponentially in time.
- (ii) We assume that initially a group of walkers, which we call the scouts, leave their nest. Along the way, they drop a trail pheromone, denoted as chemical A. The motion of the scouts is influenced by chemical A in the simple manner that is described in Sect. 3. Since the active walkers only act locally and determine their way with no additional informations, a scout can hit a food source only by chance. In that case, this particular scout begins to drop a different pheromone, chemical B, indicating the discovery of the food source. But it continues to be sensitive to chemical A, which provides local orientation, and therefore increases the chance that the scout is guided back to the nest.
- (iii) When a scout that drops chemical B should return to the nest, it recruits a number of walkers to move out. The recruits are different from the scouts only in that they are sensitive to chemical B - and not to A - when they start from the nest, but they also drop chemical A as long as they have not found any food. If a recruit hits a food source, it also begins to drop

chemical B and becomes sensitive chemical A, which should guide it back to the nest where it, indicated by dropping chemical B, can recruit new walkers.

We want to point out again, that neither the scouts nor the recruits do have any information about the location of the nest or the food sources. They only use the local orientation provided by the concentration of that chemical which they are sensitive for and they only make a local decision about the next step with no ability to store their way in an individual memory.

In order to complete our model, we have to discuss some further assumptions:

- (iv) It is known from central foragers like ants that they are able to leave a place where they don't find food and reach out for other areas. This indicates that they have at least a certain ability to increase their mobility since they have a certain aim, finding food. Active walkers, on the other hand, do not have aims and do not reflect a situation. So, they stick on their local markings even if they they did not find any food source. In order to increase the mobility of the active walkers in those cases, we assume that every walker has an individual sensitivity to follow a chemical gradient, which is related to the inverse of the temperature (or to the thermal noise) in physics. As long as the walker does not hit a food source, this sensitivity is continuously decreasing, meaning, that the walker more and more ignores the chemical detected and thus becomes able to choose also sites not visited so far. However, if the walker does not find any food source after a certain number of steps, it "dies" at a critical low sensitivity and is removed from the system. On the other hand, if the walker hits a food source, this sensitivity is set back to the initial high value and is kept constant to increase the chance that the walker finds its way back along the gradient. The switch of the level of sensitivity is accompanied with the use of the two different chemical markers, and in this particular sense reminds on chemokinesis, where the level of activity can be changed due to chemical conditions in the surrounding.
- (v) Further, the food sources could be exhausted by the visting walkers, which are assumed to carry part of them back to the nest.

The directed trails which should connect the nest with the food sources, do not exist from the very beginning; they have to be generated by the walker community in a process of self-organization. Hence, the walkers have to perform two quite different tasks, which are referred to each other: first, they have to detect food places - unknown to them, and then they have to link these places to their original starting point by forming a trail, with local chemical orientation as the only tool provided. The computer simulations outlined below should prove that the simple local rules assumed for the action of the walkers are sufficient enough to solve such a complex problem.

6 Setup for the Computer Simulations

Our simulations are carried out on a triangular lattice of size 100×100 with periodic boundary conditions. The walkers are moving on the lattice in discrete steps. Since we use a Monte-Carlo

technique, the time t is given by the number of simulation steps.

Every walker ($i = 1, \dots, N$) is characterized by two individual parameters. The first one is the drop rate, either $q_A^i(t)$ or $q_B^i(t)$, where A denotes the chemical which is dropped on the way out of the nest, and B denotes the chemical which is dropped on the way back from the food. Both drop rates decrease with time as

$$q_A^i = q_A^0 \exp\{-\beta_A (t - t_n^i)\}, \quad q_B^i = q_B^0 \exp\{-\beta_B (t - t_f^i)\} \quad (2)$$

where t_n^i, t_f^i are the times, when the walker i has started from either from the nest (n) or from the food source (f). q_A^0, q_B^0 are the initial drop rates and β_A, β_B are the decay parameters for the drop rates.

The second parameter that characterizes the walker, is the individual sensitivity, $s_i(t)$, which decreases in time as long as the walker has not found a food source:

$$s_i(t) = s_0 - ds(t - t_n^i) \quad (3)$$

where t_n^i again is the starting time of walker i from the nest, s_0 is the initial sensitivity and ds is the decrease per step. If the sensitivity s_i has reached the critical lower value, s_{min} , the walker i is removed from the system. But if, on the other hand, the walker found some food before that, the direction of its next step is reversed and its sensitivity is set back to the initial value, s_0 . In other words, $s_i = s_0$ if the walker drops the food chemical B .

The walker that moves on the triangular lattice can check for an existing chemical only on the next neighbor sites and among these only on those three sites which are in its direction of motion. This means, that in a probabilistic model the walker of course has the ability to choose its next step among the six next neighbor sites, but in the given model it can recognize a chemical only on three of them. The threshold parameters q_A^{tr}, q_B^{tr} for the recognition of the chemicals A and B are set to a low value, which is constant.

In the absence of a positive gradient of the chemical, the walker moves like a biased random walker, where α is the persistence parameter to prefer the direction of the last step. α can vary between 1 (pure random walker) and 0 (straight walk). Since every walker has six neighbor sites to choose from, with a probability $1 - (5\alpha/6)$ it prefers to go into the same direction, and with a probability $\alpha/6$ it chooses one of the other five directions. But if the walker detects a positive gradient, this will increase the probability to go towards the gradient. In our model, with a probability equal to the individual sensitivity s_i , the walker moves into the direction of the highest gradient, or with probability $(1 - s_i)$ it chooses among the remaining five directions. Among these, there exists a higher probability again that the walker would persist in moving into the direction of its last step.

Since the chemicals A and B can decompose again, the following reaction equations for the space and time dependent concentration fields $c_A(r, t), c_B(r, t)$ hold, which replace eq. 1:

$$\frac{dc_A(r, t)}{dt} = -\gamma_A c_A + Q_A(r, t), \quad \frac{dc_B(r, t)}{dt} = -\gamma_B c_B + Q_B(r, t) \quad (4)$$

where γ_A, γ_B are the decomposition rates and

$$Q_A(r, t) = \sum_{l=1}^{N_A(t)} q_A^l(t) \delta(r - r_l(t)), \quad Q_B(r, t) = \sum_{k=1}^{N_B(t)} q_B^k(t) \delta(r - r_k(t)) \quad (5)$$

indicate the production of the chemicals A or B by the walkers, which are at position r_i . $\delta(r - r_i(t))$ is again the delta function. It is assumed that N_A walkers are moving from the nest to the food source, dropping chemical A , and N_B walkers are moving back from the food source, dropping chemical B .

The initial conditions for the the simulations, discussed below, assume a nest of walkers in the center of the lattice, where, at time $t_0 = 0$, a number N_0 of walkers, the scouts, start from with a random direction. The recruitment rate is given by N_r , which is the additional number of walker that move out if a walker that is indicated by dropping chemical B , returns to the nest. The maximum number of walkers in the simulations is limited to N_m , which denotes the population size.

For the food sources two different distributions are assumed: (1) a continous food distribution at the top/bottom lines of the lattice, (2) a random distribution of five separated food sources. Both types of sources are simulated by N_F food clusters, each of a size of seven lattice sites, where F_0 is the total amount of food in each cluster. Since the sources could be exhausted by the visting walkers, we introduce the parameter df to be the amount taken away by the walker, so that all sources are exhausted after $n_{ex} = N_F F_0 / df$ visits.

To conclude the setup for the computer simulations, we give the parameters (in arbitrary units) chosen for the simulations discussed below:

$$\begin{aligned} N_0 &= 20, N_r = 5, N_m = 100, q_A^0 = q_B^0 = 80, q_A^{tr} = q_B^{tr} = 1, \beta_A = \beta_B = 0.0512, \\ s_0 &= 0.99, ds = 0.001, s_{min} = 0.5, \alpha = 0.6 \end{aligned}$$

Further we have chosen:

for simulation (1): $\gamma_a = \gamma_B = 0.001, N_f = 50, F_0/df = 55$

for simulation (2): $\gamma_a = \gamma_B = 0.01, N_f = 5, F_0/df = 550$

7 Results of Computer Simulations

In the following we discuss computer simulations for the trail formation between a nest (in the center) and two different distribution of food sources: (1) an extended food source, which is at a larger distance from the nest - this is the case, which Fig. 1 is based on, and (2) a number of separated food sources in different distances from the nest.

(1) Trunk Trail Formation to Extended Forage Areas

Figs. 3 a-f show the time evolution of the trail system for exploiting the extended food source (at the top/bottom lines of the lattice) in terms of the spatial concentration of the chemicals A (left) and B (right). The concentration is coded into a grey scale, where the deeper grey marks the higher concentration (on a logarithmic scale).

Fig. 3 a, d gives the concentration of both chemicals after the initial period. We see, that the food is already discovered by the walkers, but so far no trail exists between the food and the nest, indicated in the non-overlapping concentration fields of both components. Therefore, during the simulation, we see the walkers moving quite randomly. But, after a time lag of desorientation, the emergence of distinct trunk trails can be clearly observed in Figs. 3 b,e. and 3 c,f.

A match of the concentration fields for both chemicals A and B for the main trails shows that the walkers indeed use the same trunk trails for their movement towards the food sources and back home. The exhaustion of some food clusters and the discovering of new ones in the neighborhood results in a branching of the main trails in the vicinity of the food sources (at the top or bottom of the lattice), leading to the dendritic structures expected. The trail system observed in Figs. 3 c,f remains unchanged in its major parts - the trunk trails, although some minor trails in the vicinity of the food sources slightly shift in time - as has been reported also in the biological observations of trunk trail formation in ants.

The simulations presented in Fig. 3 in fact show two separate trail systems, one from the nest to the top, the other one to the bottom of the lattice. The emergence of both of them at the same time depends on the number of walkers available to maintain the whole trail system. Since we have a probabilistic model, the trunk trails of the upper and the lower trail system are not identical, but the dendritic structures are similar. Especially the trail system to the food sources at the bottom is, with respect to its branching structure, very similar to that drawn in Fig. 1. Thus, we conclude that the basic features of the trunk trail formation are represented by our simulation.

(2) Trunk Trail Formation to Separate Conspicuous Food Items

Figures 4(a-d) show the trunk trail formation from a central nest to five distinct food sources in terms of the spatial concentration of chemical B, which is coded again into a grey scale. In Fig 4a, we see that two of the food sources randomly placed on the lattice, have about the same distance to the nest, but the one, which - by chance - has been discovered first, will also be the one linked first to the nest. This reflects the influence of initial symmetry breaking effects.

We assumed that the food sources could be exhausted by the walkers carrying food to the nest. Once the food source vanished, the individual sensitivity of the walkers coming from the nest to the food, can not be set back to the high initial value and the walkers further increase their mobility by ignoring the trail, they reach out again, and by chance discover new food sources. But since a trail already exists, those sources have a larger probability to be discovered, which are in a close vicinity to the one that disappeared and part of the "old" trail is re-used now to link the new food source to the nest (compare Fig. 4 a,b,c).

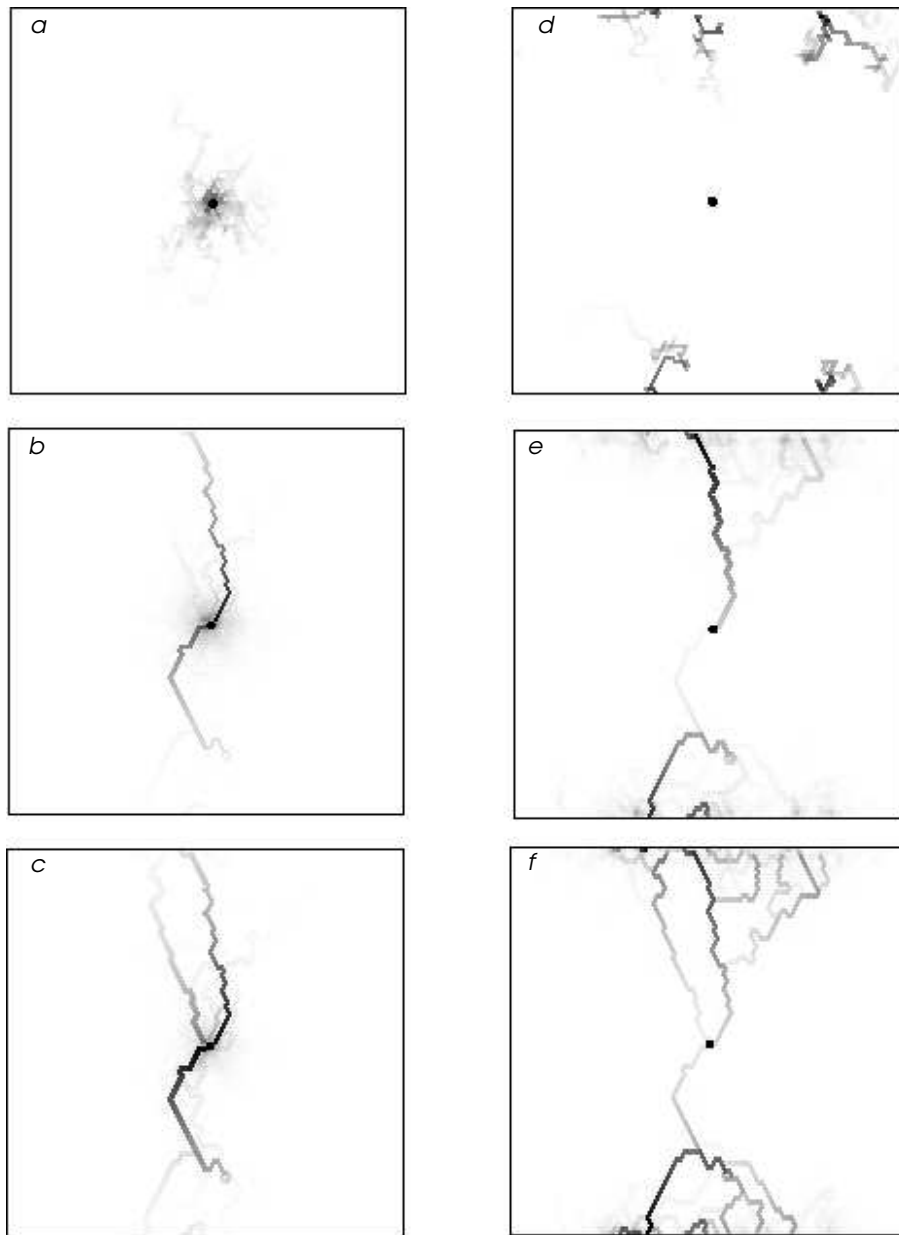


Figure 3: Formation of trails from a nest (middle) to a line of food at the top and the bottom of a lattice. (a-c) show the distribution of chemical A (see text), and (d-f) show the distribution of chemical B. The distribution is shown after 1000 steps in (a) and (d), 5000 steps in (b) and (e), and 10000 steps in (c) and (f). For the parameters of the simulation see sect. 4.

Fig. 4 b shows that at the same time also more than one sources could be linked to the nest by trunk trails. However, all trails compete for the walkers to be maintained, and the trails could

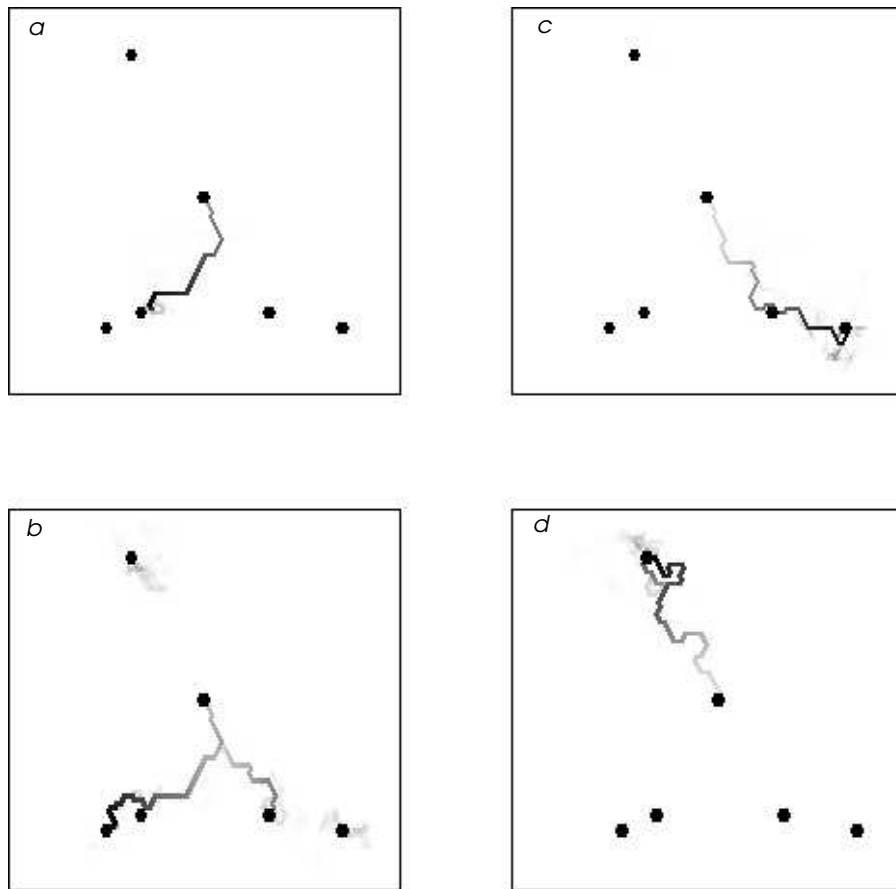


Figure 4: Formation of trails from a nest (middle) to five randomly placed food clusters. The distribution of chemical B (see text) is shown after (a) 2000, (b) 4000, (c) 8500, and (d) 15000 time steps, respectively. For the parameters of the simulation see sect. 6.

survive only if the concentration of the chemicals is above a certain critical value. To compare this fact with the simulations presented in Fig. 4 (where two trunk trail systems appeared at the same time), we have chosen for the simulations of Fig. 4 the decay rate of the chemicals to be ten times higher than for the simulations of Fig. 3. This clearly increases the selection pressure, and therefore, the coexistence of different trails only lasts for a short time. Hence, the trunk trails to the different food sources will appear one after the other, with the old trails disappearing again by decomposition because they are no longer maintained.

Since we do not have extended sources now, the trunk trails do not branch in the vicinity of the food, except in the coexistence state, when connecting different sources at the same time.

The flexibility of the model is indicated by the fact, that even after a long period of trail formation in the lower part of the lattice, the walkers are able to link the food source on the upper left side of the lattice to the nest (Fig. 4 d) and therefore finally have detected and linked all five sources

to the nest.

For the simulation shown in Fig. 4, Fig. 5 gives the cumulative number of walkers which return to the nest with food (indicated by chemical B) as a function of time.

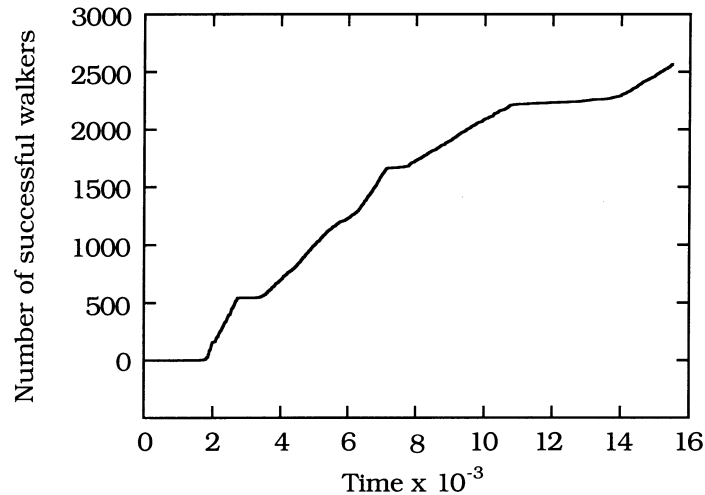


Figure 5: Cumulative number of walkers that have come back to the nest with food as a function of time (in Monte Carlo simulation steps). The data are obtained from the simulation, presented in Fig. 4

We see a large initial time lag indicating a desoriented situation, where no walker finds the way home because of the lack of a trail. But the local interactions of the walkers eventually lead to the emergence of the first trail, which is reinforced by the recruits. Hence, the concentration of chemicals A and B on the trails is increased and the process of food exploitation is selfamplified. This is indicated by an increasing number of walkers successfully returning to the nest. Once the source is exhausted, we see a new time lag needed to form the trail to the second source and so one.

Thus, we can distinguish again between two alternating dynamical stages: (i) a stage of rather random motion of the walkers (exploration of the sources), and (ii) a stage of directed motion of the walkers along the trail (exploitation of the sources).

The desorientation stage before exploiting the last source is especially long, because the walkers could not build on any previous part of a trail into that direction, whereas the desorientation stage before exploiting the third and the fourth source is very short, because of the trails which already exist into that area.

8 Conclusions

The Active Walker Model presented, is able to simulate the basic features of an interactive structure formation process. The model is flexible in two major points, which could be determined in dependence on the applications considered:

- the kind of interaction between the walkers and the surface,
- the “environmental” conditions, which can be expressed in terms of an environmental potential, that could also include topological features or changes caused by external influences (like external fields, cyclic changes).

The structures considered in this paper, are trail systems on a surface. Using the basic version of the model where the walkers only produce and respond to one kind of chemical substance, we are able to simulate track patterns, which are non-directed trails mainly used by the walkers for their movement.

In the extended model, the walkers are able to produce and to respond to two different kinds of chemicals in dependence on whether they found food sources or not. This model can simulate the formation of directed trails, which connect a starting point (nest) with other points of interest (food sources) that have to be discovered before. It turns out from the computer simulations that, for different kinds of food sources, the model generates a distinctive trail system to exploit the food sources, and performs a high flexibility in order to discover and to link new sources.

During the evolution of the trail system we can distinguish between two different stages: the first one is a rather random movement of the walkers dropping chemical almost everywhere, and no trail exists. But during the second stage, a distinct major trail appears, which is re-amplified by the walkers moving for- and backwards on the trail. This means, a trail doesn't exist from the first, it has to survive a competition process with other possible trails, where every trail not amplified enough by the walkers disappears again because of the decay of the chemical.

The basic interaction between the walkers and the surface can be considered as indirect chemical communication mediated by an external storage medium. This is a collective process in which all walkers are involved; the information one produces in terms of chemical markings, affects the decisions of the others; it could be amplified during the evolution process or disappear again.

As in every evolutionary game, also for the self-organization of trail systems critical parameters for the emergence of the structures exist. If, for instance, the decay rate for the decomposition of the chemicals is too high, or the sensitivity of the walkers is too low, they loose their local orientation and get lost, so that no trail appears. If, on the other hand, the decay rate is too low, it takes a much longer time, before a distinct trunk trail appears, because the selection pressure is too low. Or, if the sensitivity of the walkers is too high when they move out from the nest, their motion is restricted to the close vicinity of the nest, because they always follow the markings. Similar considerations hold for the local orientation of the successful walker which have to find their way back to the nest. But only if the number of recruits is large enough to maintain the whole trail system, it will keep

its distinctive overall structure intact and becomes a special kind of a quasistationary structures - as long as the food sources last.

In the model provided, the formation of trail systems is clearly a self-organizing process, based on the interactions of the walkers on a local or "microscopic" level, which could lead to the emergence of the structure as a whole on the global or "macroscopic" level. Compared to the complex "individual-based" models in ecology (Huston *et al.*, 1988, DeAngelis and Gross, 1992) the Active Random Walker model proposed here provides a very simple but efficient tool to simulate a specific structure only with a view adjustable parameters.

The major difference to biology is denoted by the fact, that the active random walkers used in the simulations, do not have individual capabilities to store and process informations about the locations of the food or the nest, or to count on navigational systems or additional guidance. They rather behave like physical particles which respond to local forces in a quite simple manner, without "implicit and explicit intelligence" (Haefner and Crist, 1994). The more suprising is the fact that these walkers are able to solve the complex task to discover and to link food sources to the nest by "knowing" nothing else than the local concentration of a chemical. With respect to the formation of trunk trails, this could indicate, that visual navigation and information storage does not nessecarilly have to be indispensable presumptions to obtain those advanced and efficient foraging patterns.

Acknowledgments

FS would like to thank DAAD for financial support during his stay at Emory University. This research was supported by a grant from the Office of Naval Research.

References

- Alt, W., 1980, Biased Random Walk Models for Chemotaxis and Related Diffusion Approximations, *J. Math. Biol.* 9, 147-177.
- Alt, W. and Hoffmann, G.(eds.), 1990, Biological Motion, Lecture Notes in Biomathematics, vol. 89 (Springer-Verlag, Berlin).
- Attygalle, A.B.; Vostrowsky, O.; Bestmann, H.J.; Steghaus-Kovac, S. and Marschwitz, U., 1988, (3R,4S)-4-Methyl-3-heptanol, the trail pheromone of the ant *Leptogenys diminuta*, *Naturwissenschaften* 75, 315-317.
- Attygalle, A.B.; Steghaus-Kovac, S., and Ahmed, V.U., 1991, cis- Isogeraniol, a recruitment pheromone of the ant *Leptogenys diminuta*, *Naturwissenschaften* 78, 90-92.
- Berg, H.C., 1983, *Random Walks in Biology*, Princeton: University Press.

- Calenbuhr, V. and Deneubourg, J.L., 1990, A model for trail following in ants: individual and collective behaviour, in: *Biological Motion*, W. Alt, G. Hoffmann (eds.), (Springer, Berlin), pp. 453-469.
- Crist, Th.O. and Haefner, J.W., 1994, Spatial Model of Movement and Foraging in Harvester Ants (*Pogonomyrmex*) (II): The Roles of Environment and Seed Dispersion, *J. theor. Biol.* 166, 315-323.
- DeAngelis, D.L.; Gross, L.J. (eds.), 1992, *Individual-based Models and Approaches in Ecology: Populations, Communities, and Ecosystems* (Chapman and Hall, New York).
- Deneubourg, J.L.; Goss, S.; Franks, N. and Pasteels, J.M., 1989, The Blind Leading the Blind: Modeling Chemically Mediated Army Ant Raid Patterns, *J. Insect Behavior* 2/5, 719-725.
- Edelstein-Keshet, L., 1994, Simple models for trail following behaviour: Trunk trails versus individual foragers, *J. Math. Biol.* 32, 303-328.
- Edelstein-Keshet, L.; Watmough, J. and Ermentrout, G. Bard, 1995, Trail following in ants: individual properties determine population behaviour, *Behav. Ecol Sociobiol* 36, 119-133.
- Family, F. and Gould, H., 1984, Polymer chain statistics and universality: Crossover from random to self-avoiding walks, *J. Chem. Phys.* 80/8, 3892-3897.
- Franks, N.; Gomez, N.; Goss, S. and Deneubourg, J.L., 1991, The Blind Leading the Blind in Army Ant Raid Patterns: Testing a Model of Self-Organization (*Hymenoptera: Formicidae*), *J. Insect Behavior* 4/5, 583-607.
- Fürth, R., 1920, Die Brownsche Bewegung bei Berücksichtigung einer Persistenz der Bewegungsrichtung. Mit Anwendungen auf die Bewegung lebender Infusorien, *Z. Phys.* II/3, 244-256.
- Goss, S; Aron, S.; Deneubourg, J.L.; Pasteels, J.M., 1989, Self-Organized Shortcuts in the Argentine Ant, *Naturwissenschaften* 76, 579-581.
- Haefner, J.W. and Crist, T.O., 1994, Spatial Model of Movement and Foraging in Harvester Ants (*Pogonomyrmex*) (I): The Roles of Memory and Communication, *J. theor. Biol.* 166, 299-313.
- Hölldobler, B. and Möglich, M., 1980, The foraging system of *Pheidole militicida* (*Hymenoptera: Formicidae*), *Insectes Sociaux* 27/3, 237-264.
- Hölldobler, B.; Wilson, E.O., 1990, *The Ants*, (Belknap, Cambridge, MA).
- Huston, M., DeAngelis, D.; Post, W., 1988, New computer models unify ecological theory, *BioSci.* 38, 682-691.
- Kayser, D.R.; Aberle, L.K.; Pochy, R.D. and Lam, L., 1992, Active walker models: tracks and landscapes, *Physica A* 191, 17-24.

- Langton, C.G. (Ed.), 1994, *Artificial Life III.*, Proc. Workshop on Artificial Life, June 1992, Reading, MA: Addison-Wesley.
- Lam, L., 1995, Active Walker Models for Complex Systems, *Chaos, Solitons & Fractals* 6, 267-285.
- Lam, L. and Pochy, R., 1993, Active-Walker Models: Growth and Form in Nonequilibrium Systems, *Computers in Physics* 7, 534-541.
- Maes, Pattie (ed.), 1992, *Designing Autonomous Agents. Theory and Practice From Biology to Engineering and Back*, (MIT Press, Cambridge, MA).
- Maschwitz, U. and Mühlenberg, M., 1975, Zur Jagdstrategie einiger orientalischer *Leptogenys*-Arten (*Formicidae: Ponerinae*), *Oecologia* 38, 65-83.
- Meyer, J.-A. and Wilson, S.W. (eds.), 1991, *From Animals to Animats*, Proc. 1st Intern. Conf. on Simulation of Adaptive Behavior, (MIT Press, Cambridge, MA).
- Müller, M. and Wehner, R., 1988, Path integration in desert ants, *Cataglyphis fortis*, *Proc. Natl. Acad. Sci. USA* 85, 5287-5290.
- Payne, T.L.; Birch, M.C. and Kennedy, C.E.J. (eds.), 1986, *Mechanisms in insect olfaction* (Clarendon Press, Oxford).
- Pricer, J.L., 1908, The life history of the carpenter ant, *Biol. Bull. Mar. Biol. Lab. Woods Hole*, 14, 177-218.
- Rettenmeyer, C.W., 1963, Behavioral studies of army ants, *Univ. Kans. Sci. Bull.* 44, 281-465.
- Schimanski-Geier, L.; Schweitzer, F. and Mieth, M., 1996, Interactive Structure Formation with Active Brownian Particles, in: *Selforganization of Complex Structures: From Individual to Collective Dynamics*, F. Schweitzer, (ed.) (Gordon and Breach, London), in press.
- Schneirla, T.C., 1933, Studies of army ants in Panama, *J. Comp. Psychol.* 15, 267-299.
- Schneirla, T.C., 1940, Further studies on the army ant behavior pattern: Mass organization in the swarm-raiders, *J. Comp. Psychol.* 29, 401-461.
- Schweitzer, F. and Schimansky-Geier, L., 1994, Clustering of active walkers in a two-component system, *Physica A* 206, 359-379.
- Stevens, A., 1990, Simulations of the gliding behavior and aggregation of Myxobacteria, in: *Biological Motion*, W. Alt, G. Hoffmann (eds.), (Springer, Berlin), pp. 548-555.
- Stevens, A. and Schweitzer, F., 1996, Aggregation of Individuals Induced by Diffusing and Non-diffusing Media, in: *Mechanisms of Cell and Tissue Motion*, W. Alt, A. Deutsch, G. Dunn (eds.) (Birkhäuser, Basel), in press.
- Sudd, J.H., and Franks, N.R., 1987, *The Behavioural Ecology of Ants* (Blackie, Glasgow).

- Wehner, R., 1987, Spatial Organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namib Desert), in: From individual to collective behavior, J.M. Pasteels, J.L. Deneubourg (eds.), (Birkhäuser, Basel, pp. 15-42).
- Wehner, R., 1992, Arthropods, in: Animal Homing, F. Papi (ed.) (Chapman and Hall, London), pp. 45-144.
- Wehner, R. and Menzel, R., 1990, Do insects have cognitive maps?, *Annual Rev. Neurosci.* 13, 403-414.
- Wehner, R. and Räber, R., 1979, Visual spatial memory in desert ants, *Cataglyphis bicolor* (*Hymenoptera, Formicidae*), *Experientia* 35, 1569-1571.
- Wehner, R. and Wehner, S., 1990, Path integration in desert ants. Approaching a long-standing puzzle in insect navigation, *Monitore zool. ital. (NS)* 20, 309-331.
- Wilson, E.O., 1971, *The Insect Societies* (Belknap, Cambridge, MA).