Collective Intelligence in Insect Colonies by means of Self-Organization

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Abstract

Colonies of insects are well-organized entities, displaying remarkable collective abilities. For example, the internal temperature of honeybee colonies is precisely regulated to within 0.5° of 35° C, despite wide fluctuations in ambient temperature (Heinrich 1985). Certain African termites build enormous, intricate nests which maintain an even internal temperature and high humidity while permitting adequate oxygen and carbon dioxide exchange with the environment (Lüscher 1961). One usually associates these kind of precise regulatory capabilities with multicellular organisms such as mammals where body temperature, glucose and electrolyte levels, and respiratory exchange are carefully maintained by intricate physiological mechanisms involving circulatory and neural pathways, as well as central processing by the brain.

In this regard, a colony of social insects presents a challenging paradox: The colony exhibits complex patterns of social behavior permitting exact homeostatic adjustments and the creation of complex nest structures. However, the colony appears to lack the requisite physiological machinery and collective intelligence to accomplish these tasks.

The self-organization approach to insect societies shows how higher-order, colony-level complexity arises not through the sophistication and complexity of the individual workers in the colony, but as an automatic consequence of large numbers of simple subunits interacting concurrently. Three examples of self-organizing processes in social insects are discussed: (1) Pattern formation on the combs of honey bee colonies, (2) Collective nectar source selection by honey bees, and (3) Brood sorting in ants. These examples show how simple subunits interacting in parallel and guided by simple probabilistic rules of interaction can generate complex collective behaviors and patterns.

Introduction

How does the colony efficiently apportion its work force among the various tasks required for colony survival? How are honey bee foragers able to exploit the best among an array of ephemeral food sources in the environment? How does a swarm of bees discover and agree upon an appropriate nest site from many potential sites in the field?

The colony consists of thousands of loosely assembled individuals each functioning rather autonomously. It is inconceivable that an individual colony member could acquire detailed information about the state of the entire colony, and play a central role in monitoring and directing the activities of other colony members. In an insect colony, there are no foreman, consultants or supervisors which gather and process information, and organize the colony's activities.

A useful approach to understanding colony organization is to view the insect colony as a complex system. Self-organizing higher-order phenomena may emerge spontaneously in such a system when (1) large numbers of individual subunits (2) using behavioral rules based upon local (versus global) information (3) act simultaneously and independently.

A useful approach to analyzing a particular colony-level phenomenon in insect colonies is as follows: (1) Identify an important colony-level process whose mechanism is poorly understood. (2) Identify the individual subunits involved in the process. (3) Identify the informational input to the subunits. (4) Characterize the effect of the input on the subunits. (5) Simulate the hypothesized system for confirmation.

Consider the example of colony thermoregulation of a honey bee swarm. Here the subunits are all individual worker bees in the swarm. The informational input in this case may be the bee's monitoring of its own temperature and that of its immediate local surroundings. The effect of this input is the set of behavioral and physiological activities used by the individual bee.

Through simulation of the system of swarm thermoregulation, one can ask whether the proposed model generates the observed colony-level process? For example, does the simulation result in the observed temperature profile under a normal range of ambient temperatures? If not, this may suggest that further experiments and observations are indicated to verify the accuracy of steps (2)-(4). Computer simulations are crucial at this stage because when large numbers of subunits interact, even in quite simple ways, the outcome is difficult, if not impossible to predict. The output of complex systems are often non-intuitive and unexpected.

A model of a colony-level process is merely an hypothesis stated in a rigorous mathematical manner. But unlike a verbal statement of a hypothesis, it is dynamic in that it actually does something. By simulating the model on the computer, one generates a specific output which serves as a test of the model. If the output matches the colony-level process under consideration, then one has increased confidence that the original observations and experiments correctly revealed the components of the process and their proper interactions.

Thus, models are tools for testing hypotheses. They are particularly useful since they require that the interactions among all the components be precisely specified. A facile verbal argument can easily hand-wave its way around a complete explanation of a process, but in a computer simulation each component of the process and its interactions must be explicitly defined. Lacking even the smallest detail, a simulation does nothing because a computer program is like a chain. Every link is critical to the integrity of the whole.

This approach to analyzing a colony-level process as a complex system can be characterized as a bottom-up rather than top-down. First the components of the system and their interactions are characterized based upon field observations and experiments. Then these components are assembled in a computer model. Once you are confident that nothing crucial has been left out, the model then permits assessment of the significance

of each of the system's components and their interactions. It may also provide information about aspects of the internal dynamics of the system that are not readily available through field observations or experiments.

One difficulty with the bottom-up approach is that it requires a very detailed understanding of the components of a process in order to achieve a real understanding of how the colony-level process emerges. For this reason, it is often tempting to use a top-down approach. One starts with the same colony-level phenomenon, but lacks a complete understanding of the components or their interactions either because one is at an early stage of examination, or because some components of the system resist analysis. Instead one guesses what the components might be and how they might interact. One hopes to hit upon a model that works (reproduces the observed colony-level process). One can then conclude that the proposed model may have some relationship to the actual mechanism. Unfortunately, even if one does come up with a model that gives a good prediction of the colony-level phenomenon, one has little confidence that the proposed mechanism has any bearing on reality because many different hypothesized models may all be capable of mimicking properties of the system.

In practice, one often resorts to a combination bottom-up and top-down approach. Ideally one would study a system in as much detail as possible, extracting as many of the components and interactions based upon direct observation. Gaps in one's knowledge can be filled in with hypotheses. If the model simulation behaves as expected, further observations and experiments can be designed to determine whether the hypothesized components and interactions are valid.

Examples of Self-Organization in Insect Societies

I will now briefly present 3 examples of the application of this approach:
1) Self-organizing pattern formation on the combs of honey bee colonies
2) Collective nectar foraging in honey bees
3) Brood sorting in ants:

Self-organizing pattern formation on the combs of honey bee colonies

A honey bee colony comprises approximately 25,000 worker bees and a single queen. In addition to the adult bees there is immature brood, consisting of developing eggs, larvae and pupae, as well as a variable amount of accumulated food, namely honey and pollen. These are stored within the hive in a series of parallel wax combs subdivided into approximately 100,000 cells. A characteristic well-organized pattern develops on the combs, consisting of three distinct concentric regions - a central brood area, a surrounding rim of pollen, and a large peripheral region of honey.

The well-organized pattern suggests a possible adaptive function. A compact brood area may help to ensure a precisely regulated incubation temperature for the brood and may facilitate efficient egg laying by the queen. The location of pollen in the rim adjacent to the brood area, where it is readily accessible to the nurse bees, may promote efficient feeding of the nearby larvae.

The pattern is not only well-organized, but also consistent throughout the season. This feature may also be adaptive. Each day honey and pollen from tens of thousands of foraging trips are deposited into the cells, stores of honey and pollen cells are continually consumed, hundreds of eggs are laid, and mature adult bees emerge from their cells. Despite the constant turnover in which cells are often refilled with something different, a stable pattern persists.

The presumed adaptive significance of the pattern raises the important question of what mechanisms account for its origin and maintenance. How does this colony-level pattern emerge from the activities of thousands of bees? I present a model of pattern formation based upon self-organization.
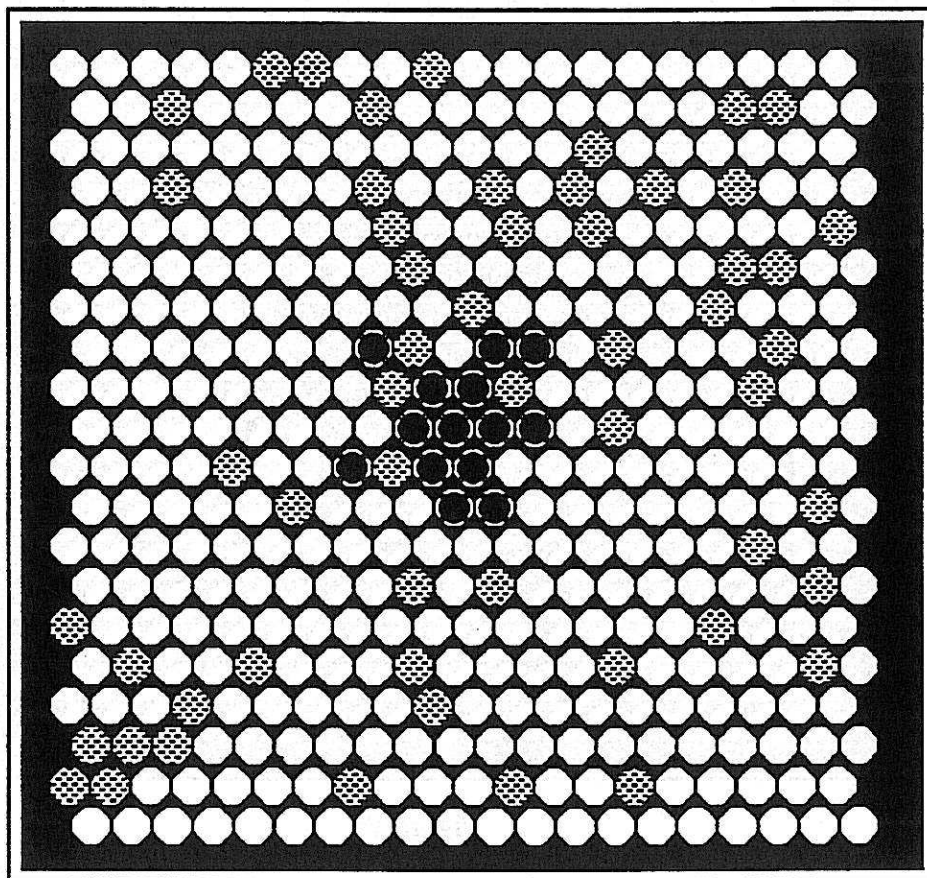
Figure 1a

This model is derived from experimentally determined behaviors of honey bees (Camazine 1991). The behavioral rules can be summarized as follows:

(1) The queen moves over the combs rather unsystematically searching for empty cells in which to lay eggs. Approximately 95% of eggs are deposited within 3 cell lengths of another brood cell. The queen lays between 1000 and 2000 eggs per day.

(2) Once an egg is laid in a cell, it remains in place for the 21 days required for development to the adult stage.

(3) Honey and pollen are deposited in randomly selected cells, either empty or partially filled with the same substance.

(4) The ratio of honey removal to honey input is approximately 0.6. The ratio of pollen removal to pollen input is approximately 0.95. The average ratio of pollen input to honey input is approximately 0.25.

(5) Honey and pollen are removed from cells in an amount proportional to the number of surrounding cells containing brood.

Note that each of these simple rules is based entirely on local information, namely the content of the cell itself and that of its closely neighboring cells. This feature makes the system well suited to incorporate the behavioral rules into a probabilistic cellular automaton model. The model exhibits the characteristic concentric pattern of brood,
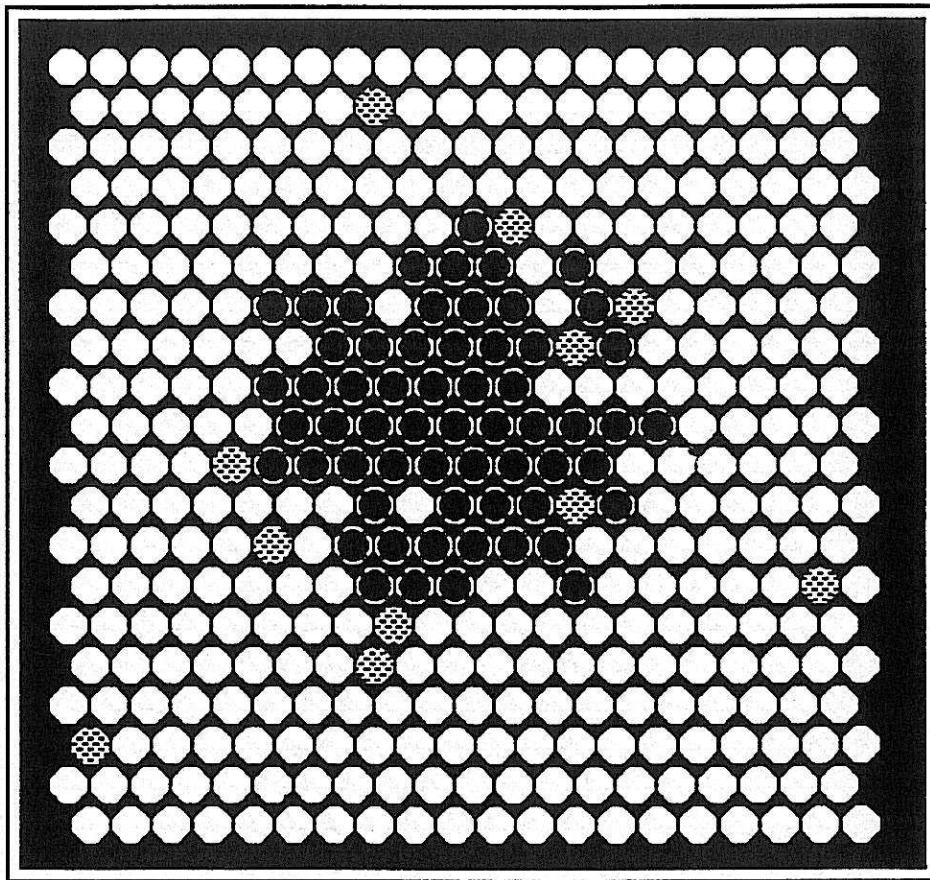
Figure 1b

pollen and honey under a wide range of parameter values. Figure 1 shows the process of pattern formation on a small section of comb from the center of the colony. In the initial stages of the simulation (Figure 1a) pollen (gray circles) and honey (white circles) are found throughout the comb as bees deposit their loads randomly on the empty frame. At the same time, the queen wanders over the frame from a central starting point laying eggs (black circles) in empty cells nearby other cells containing eggs. The result is a haphazard mix of honey and pollen, with a central region sparsely occupied with eggs. Many of the cells interspersed among the eggs contain honey and pollen. This is the early disorganized stage. As the simulation proceeds (Figure 1b) pollen begins to disappear from the periphery, resulting in a solid region of honey. In addition, both pollen and honey disappear from the center of the comb leaving a compact roughly circular brood area. A band of pollen develops between the brood and the honey. In this mature stage (Figure 1c) the characteristic well-organized pattern appears. How does this transformation occur? Three processes contribute to the pattern formation. First, a compact brood area results from the preferential removal of honey and pollen nearby brood. This continually provides empty cells in the brood area into which the queen lays eggs. A second process explains the segregation of honey and pollen in the periphery. Since both are deposited randomly, initially both pollen and honey fill the comb. However, since less pollen is collected than honey and since pollen has a greater turnover rate than honey, pollen cells are more likely to be emptied than honey cells, and these empty cells will be more likely refilled with honey. Gradually any pollen deposited in the periphery is removed, leaving this region almost entirely honey. So, where is the pollen stored? The only cells available for pollen are those with a high turnover rate.
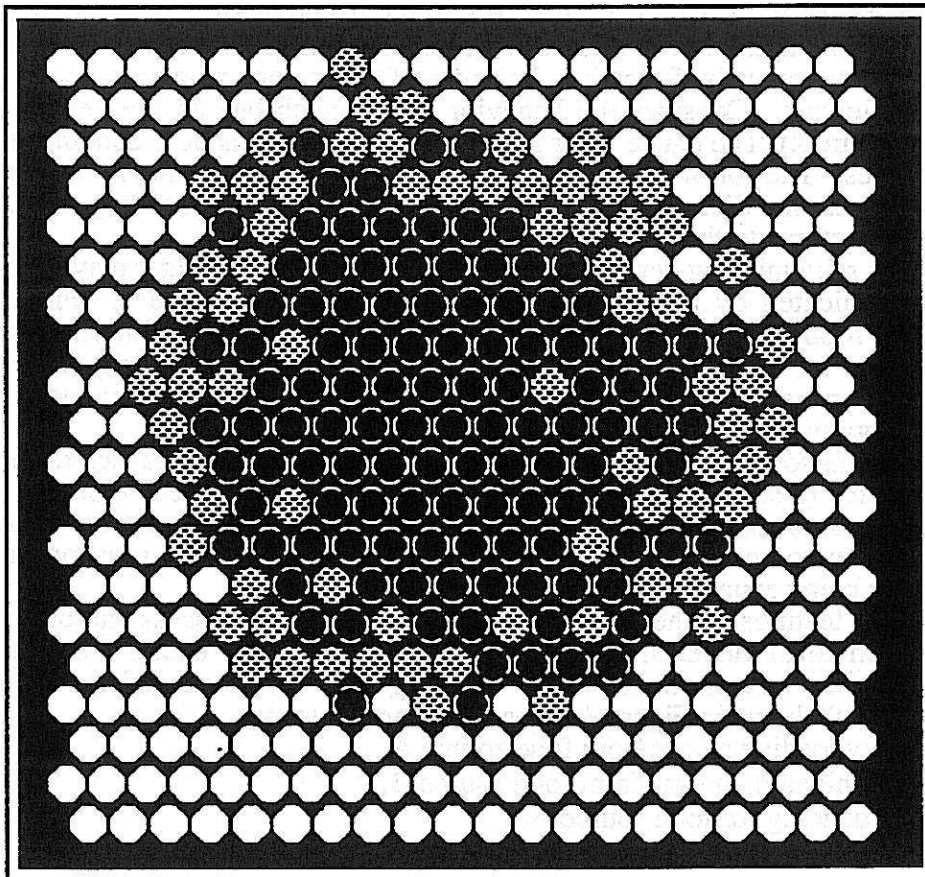
Figure 1c

These are the cells at the periphery of the brood area. Once a cell is occupied by an egg, it is "reserved" as a brood cell for the next 21 days of honey bee development. But in the interface zone between the central brood and the peripheral region of honey, the preferential removal of honey and pollen continually provides a region where cells are being emptied at a relatively high rate. These cells are available for pollen

In this self-organizing system, there is no need to specify particular locations for eggs, pollen or honey, nor do the bees require any global knowledge about the developing pattern to which they are contributing. Following a few simple rules based upon local information the comb pattern emerges automatically through the dynamic interactions of the bees.

A model of collective nectar source selection in honey bees

A honey bee colony chooses among different nectar sources in the field, selectively foraging from those which are most profitable. This model, based on Camazine and Sneyd (1991) describes the colony's decision-making process, and consists of a system of non-linear differential equations describing the activities of the foraging bees. Parameter estimates are based on previously published data (Seeley et al. 1991). Numerical solutions of the equations agree closely with experimental observations. A model of the activities of the individual bees is also presented in the form of a one-dimensional probabilistic cellular automaton. This model illustrates how the individual

activities of the foraging bees contributes to the overall pattern of colony-level foraging presented in the differential equation model.

We begin with a pool of foragers lacking knowledge of the potential nectar sources available in the field. Each of these bees is called a "follower bee" because she reaches a nectar source by following the dance of a nest mate who has already discovered a patch of flowers. Consider the behavior of one such bee as she begins her day of foraging (Figure 2). The dance floor area of the hive contains bees dancing for different nectar sources. The follower bee selects a dancer for nectar source A. After following the bee's dances, she flies to that nectar source. Upon arrival, the forager gathers a load of nectar and returns to the hive.

After relinquishing her nectar to a food storer bee, the forager may do one of three things, as indicated by the branch points (diamonds) in Figure 2. First, she may abandon the food source and return to the pool of uncommitted followers. Alternatively, if she decides to continue to forage from the nectar source, she may either perform recruitment dances before returning to her patch of flowers or continue to forage at the food source without recruiting nest mates.

Many factors affect the probability that an individual bee dances for or abandons the food source (Seeley 1986, Seeley et al. 1991): nectar sweetness, distance to the food source, ease of nectar collection, colony intake rate. In this model, for simplicity, we consider nectar sources that differ in quality only with respect to sugar concentration, all other factors being equal.

These features of the colony-level decision-making process can be incorporated into a mathematical model of foragers choosing between two nectar sources. First, we assume that, at any moment, each foraging bee is in one of the seven places (compartments) shown in Figure 3. These compartments are:

H_a: unloading nectar from food source A,
H_b: unloading nectar from food source B,
D_a: dancing for food source A,
D_b: dancing for food source B,
A: feeding at food source A
B: feeding at food source B,
F: following a dancer.

The dance floor (shaded area in Figure 3) contains three of the compartments: those bees dancing for A, those bees dancing for B, and those bees following a dancer. In contrast to Figure 2, note that Figure 3 consists of two separate cycles, one for each food source, with the follower compartment, F, the only one shared by the two cycles. Thus, bees from one feeder can switch over to the other feeder only by passing through the dance floor and following a dancer for the other food source. The figure suggests that the dance area plays the central role in the decision-making process. Whatever information is transferred among the bees is assumed to take place here.

Two factors affect the proportion of bees in each of these 7 compartments: (1) The rate at which a bee moves from one location to another, and (2) The probability that a bee takes one or the other fork at the five branch points (diamonds) of Figure 3. For each of the 7 compartments we specify a rate constant p_{1-7}, in units sec^{-1}. Thus, the average time a bee stays in A is given by $1/p_3$, and similarly for the other compartments. The values for these rate constants are given in Seeley et al. 1991.

We next consider the movement of bees at the branch points. The first branch point occurs after a bee has unloaded her nectar in the hive. Here, a bee may desert the nectar source and return to the dance floor to follow another dancer. The fraction of the bees that abandon their food source (or the probability of any one bee doing so) is denoted by the function f_x, which we call the abandonment function. f_x is a function of the quality of the food source, and thus the fraction, $f_x{}^a$, indicates the probability that a
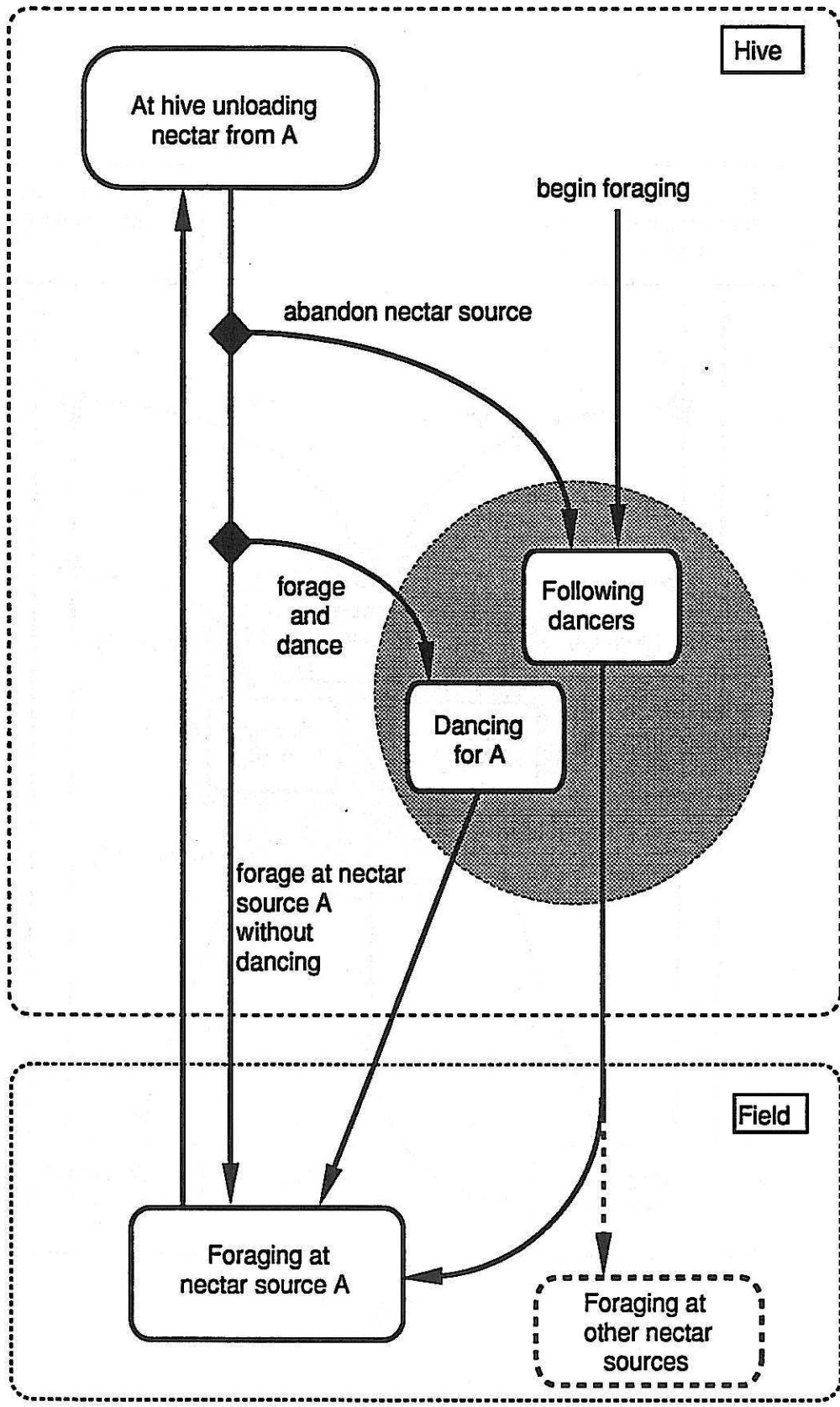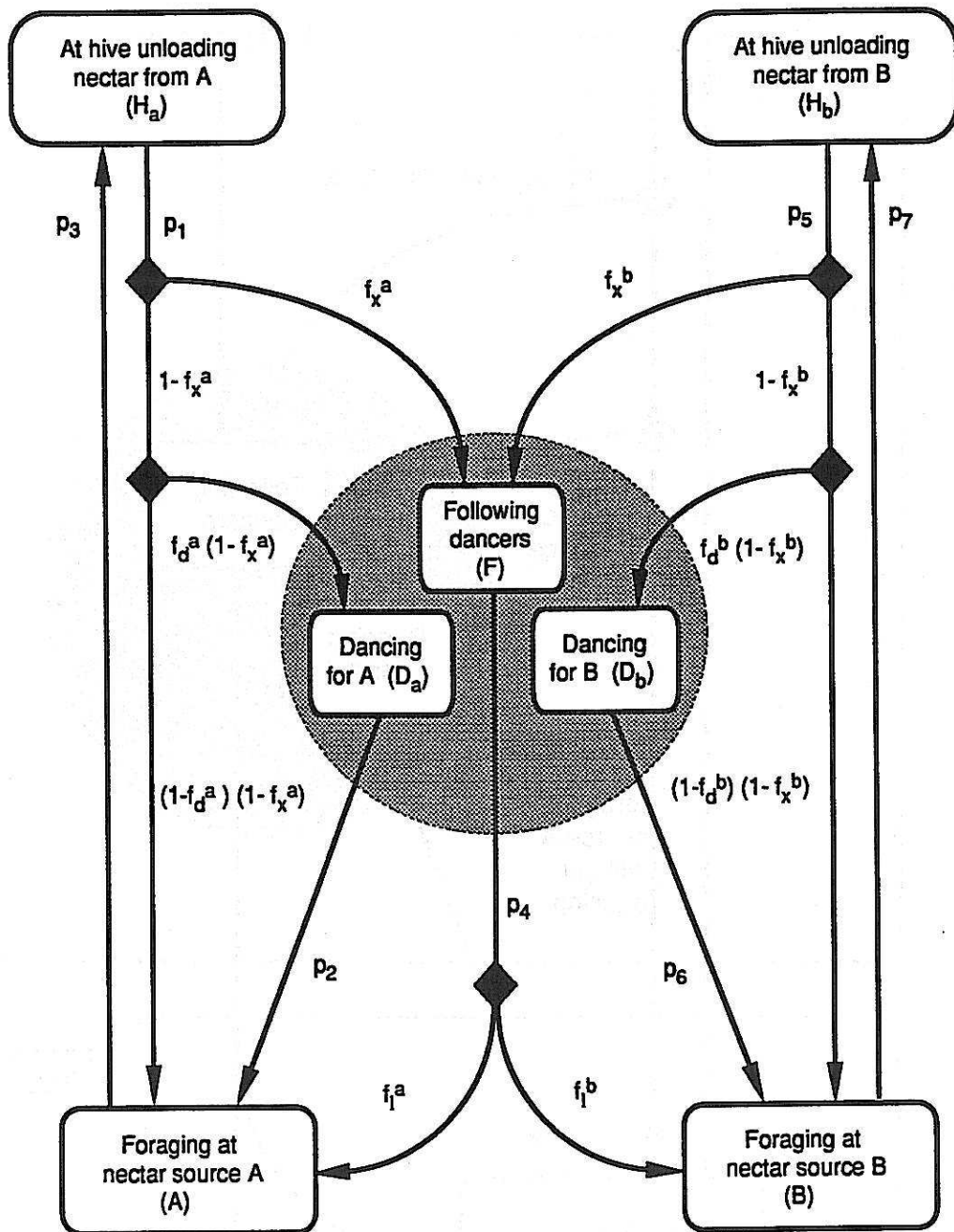
Figure 2

At hive unloading nectar from A (H_a)

At hive unloading nectar from B (H_b)

p_3 p_1

p_5 p_7

f_x^a

f_x^b

$1 - f_x^a$

$1 - f_x^b$

Following dancers (F)

$f_d^a (1 - f_x^a)$

$f_d^b (1 - f_x^b)$

Dancing for A (D_a)

Dancing for B (D_b)

$(1 - f_d^a)(1 - f_x^a)$

$(1 - f_d^b)(1 - f_x^b)$

p_4

p_2

p_6

f_l^a

f_l^b

Foraging at nectar source A (A)

Foraging at nectar source B (B)

Figure 3

bee, upon leaving H_a, will abandon nectar source A to become a follower. Abandonment diminishes the number of bees committed to a food source and provides a pool of uncommitted bees which follow dancers for one nectar source or the other.

The second branch point determines the proportion of the committed bees that dance for the nectar source they have just visited. Although at the second branch point there is no filtering of bees away from the food source to which they are committed, this branch point affects the probability with which an uncommitted forager follows a dancer for one or the other food source, as described below. The probability that a bee becomes a dancer for her food source is denoted by the function f_d, the dancing function. As for the abandonment function, its value depends on the quality of the food source, with $f_d{}^a$ indicating the probability that a bee foraging at nectar source A performs recruitment dances.

The third branch point occurs on the dance floor when bees follow dancers for one or another nectar source. The fraction of the follower bees leaving the dance floor to go to food source A is denoted by the function $f_l{}^a$, the following function. A bee entering the dance area randomly encounters dancers, and follows the first dancer she encounters. In the situation of just two nectar sources, A and B, the probability of a follower encountering dancers for A can be roughly estimated by $D_a/(D_a + D_b)$ where D_a and D_b are the number of bees in each of the dance compartments A and B, respectively. However, since only a portion of a bee's time in the dance area is actually spent dancing, it is necessary to multiply D_a and D_b in the above expression by the proportion of time that the foragers actually dance. These fractions are denoted by τ_a and τ_b. Thus $f_l{}^a = D_a\tau_a/(D_a\tau_a + D_b\tau_b)$. This fraction takes into account the number of dancers for each food source as well as the time spent dancing, and thus indicates the proportion of the total dancing for each nectar source.

Using the parameter values in Seeley et al., 1991, we can determine how well the model's predictions correspond with results of actual field experiments. Figure 4a shows the results of an actual experiment (Seeley et al. 1991) and Figure 4b shows the computed solutions of the model.

The differential equation model does not track the activities of individual foragers, making it difficult to appreciate the behavioral pattern of the foragers as they are recruited to nectar sources and abandon other sources. This can be visualized using a probabilistic cellular automaton model based upon the same probabilities of dancing, abandoning, and following used in the differential equation model. In Figure 5, the initial state of each individual forager bee is shown as a square cell in the top row of the figure. Each bee can be in one of 3 states: either committed to feeder A (white), committed to feeder B (black) or uncommitted (gray). Each iteration of the model represents one cycle of a bee's returning to the hive and making a decision to either remain committed to her feeder or to abandon the feeder and become a follower bee. A follower bee goes to the dance area and randomly selects a bee dancing for one or the other feeder. Moving down, each cell in a column displays the activity of an individual bee over time.

As shown in Figure 5, the cohort of foragers quickly "locks in" on the best food source (feeder A, shown as white). This occurs because bees for feeder B tend to abandon their food source and become uncommitted follower bees, and uncommitted bees tend to switch to feeder A. The model demonstrates how differential rates of dancing and abandonment based upon nectar source quality create a positive feedback system that rapidly filters the majority of uncommitted bees to the best food source. The model supports the view that selective exploitation of the most profitable nectar sources occurs through an autocatalytic, self-organizing process.
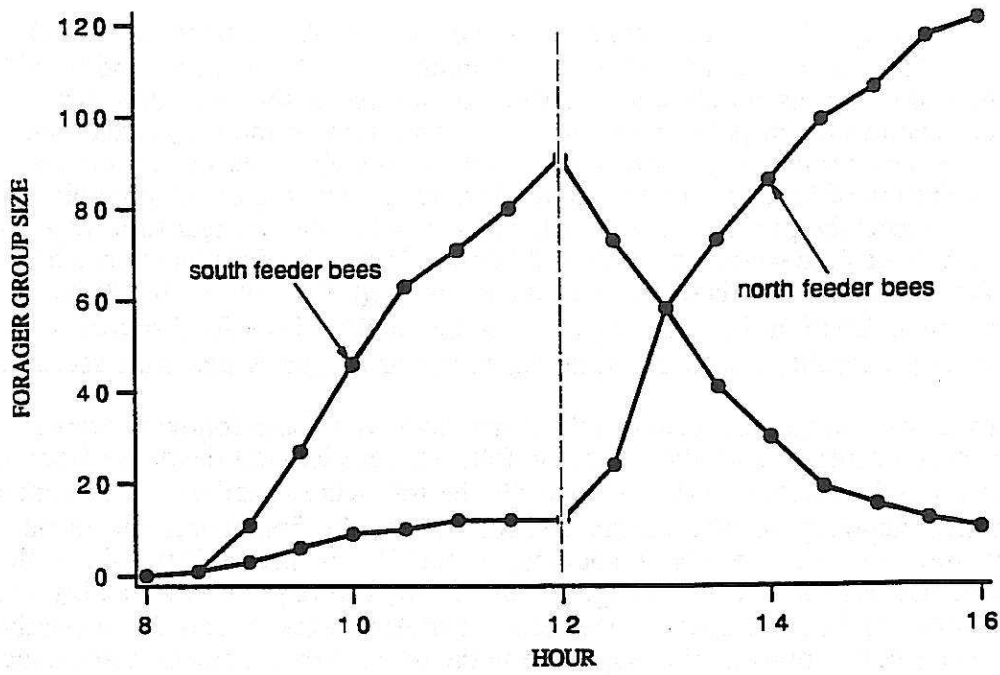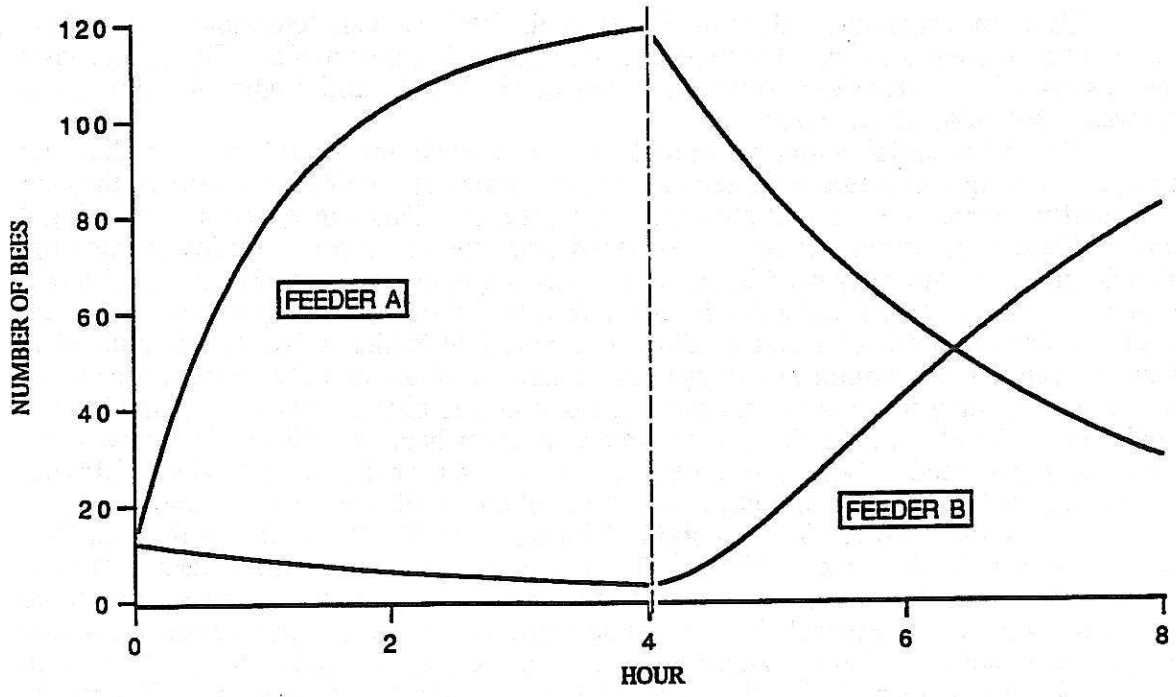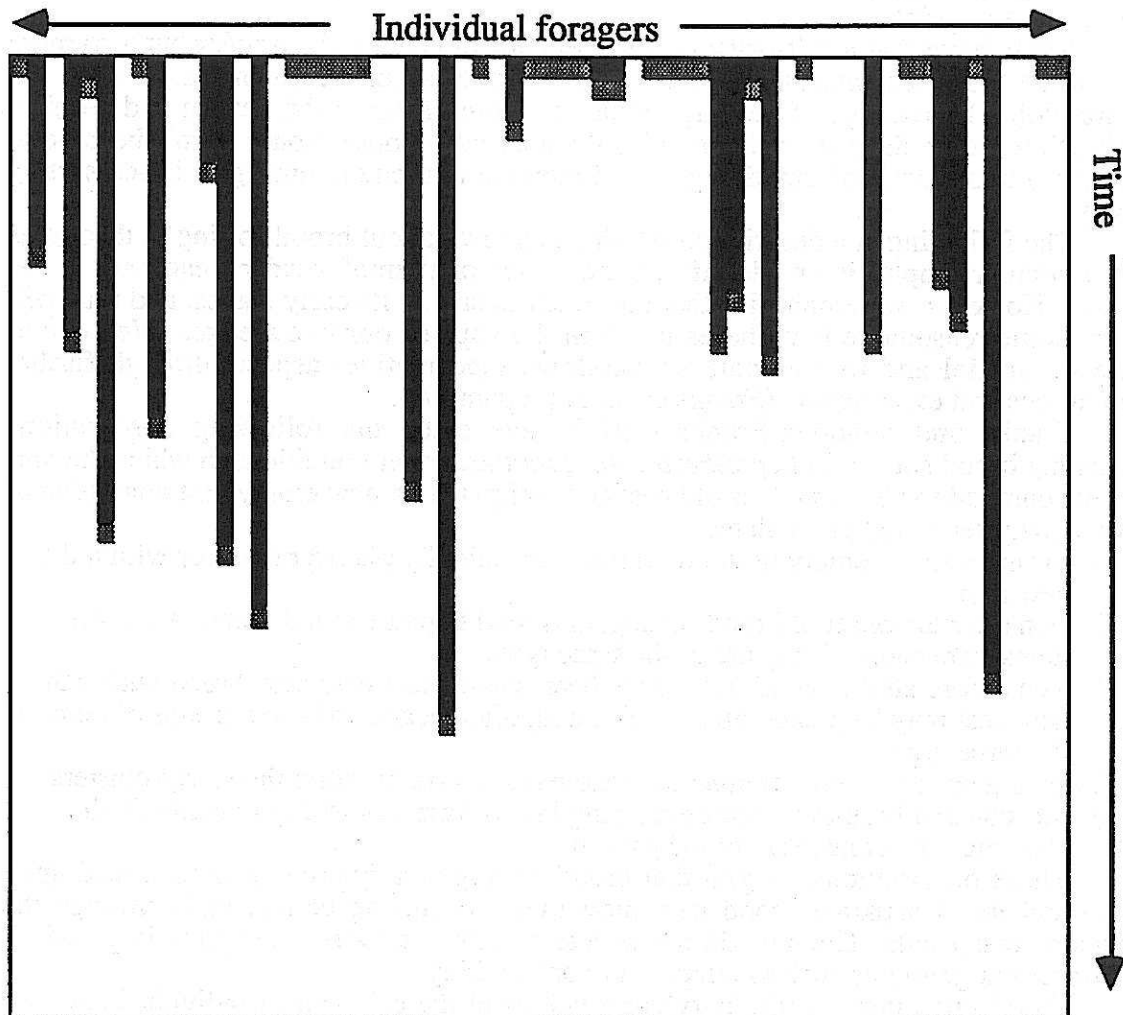
Figure 4a

Figure 4b

Figure 5

Brood sorting by ants

    Leptothorax unifasciatus ant colonies occupy flat crevices in rocks. Their brood is kept in a single cluster arranged in a distinct pattern of concentric rings. Eggs and micro-larvae form the center of the cluster with successively larger larvae arranged in radial bands away from the center of the brood cluster. An exception is the band of prepupae and pupae which are placed in an intermediate position between the largest, most peripheral larvae and the more centrally-located medium sized larvae. If the patterned arrangement of brood is experimentally disorganized, the ants will re-sort the brood over the course of several hours (Franks and Sendova-Franks 1992).

    What is the mechanism of brood sorting used by the ants? The approach is to ask whether brood sorting can be explained by a process of self-organization. In other words, can brood sorting be explained through the behaviors of individual ants each acting autonomously following simple rules based upon local information?

    An alternative hypothesis of pattern formation would posit a pattern template which the ants follow. In other words, the pattern forms as the result of ants placing each class of brood in particular locations based upon a pre-specified blueprint or plan. If the ants have some means of knowing where to place each type of brood, the concentric

pattern could arise simply as a consequence of the ants following the orderly arrangement latent in the blueprint.

We believe that a self-organization mechanism is not only simpler but also more likely to be the actual mechanism used by the ants in sorting their brood. It does not require global knowledge of the large-scale structure of the brood pattern and requires less intelligence on the part of the individual ant as each employs only simple behavioral rules based upon local information gathered moment to moment during its brood sorting activity.

The following is a description of what is known about brood sorting in these ants with particular emphasis on identifying the "rules of thumb" used by each ant in the process. However, we emphasize that this study is still in its early stages, and thus will require some reasonable hypotheses to fill in the gaps of our knowledge. We hope to refine the model and to eliminate its top-down (speculative) aspects through further observations and experiments (Franks et al., in preparation).

Franks and Sendova-Franks (1992) have made the following observations concerning brood sorting in *Leptothorax unifasciatus*, under conditions in which the ants were encouraged to abandon their old nest and emigrate to a new empty nest consisting of two narrowly separated glass plates:

1) Starting with an empty nest, brood items are initially placed randomly within the new nest
2) Soon after the onset of brood sorting, ants tend to place brood items near other items, especially if they are of the same type.
3) Even before all the brood items have been carried to a new nest, brood within the new nest may be picked up and relocated, often nearer to larger groups of items of the same type.
4) Items seem to be more frequently removed from small rather than large clusters.
5) Ants constantly re-sort their developing brood from day to day to maintain the characteristic concentric brood pattern

These observations suggest that brood sorting is a dynamic process based upon large numbers of separate brood item movements occurring concurrently through the actions of many ants. The ants do not appear to utilize a pattern template imposed by environmental gradients such as temperature or humidity.

Based upon these preliminary observations of the behavior of individual ants, we propose a model which incorporates most of these details. It is similar to the previous model presented by Deneubourg et al. (1991) in that sorting is achieved without either hierarchical decision making, communication between individuals, or any externally imposed template of the pattern. The two behavioral rules of the ants in the Deneubourg model are that (1) if a brood item is isolated, it is more likely to be picked up by an ant, and (2) when carrying an object, the probability that an ant will deposit the item is greater if there are more of the same brood type in the immediate neighborhood.

The rules proposed here are slightly different, but both models incorporate the ideas of parallel (concurrent) activities of autonomous ants following simple rules based upon local information. The two rules programmed into the simulated ants of the Deneubourg model are basically an implementation of observations 2,3 and 4 above without any top-down modeling assumptions about the behavior of the ants. Unfortunately, those two rules are insufficient to generate concentric bands of brood, although they do result in the segregation of different brood types.

The model presented here was developed for two reasons. First, it corresponds better with the observed pattern because it generates concentric regions of brood. The key behavioral rule in both models that generates pattern is a positive feedback mechanism in which brood objects are placed nearby items of the same type. This rule of "like sorts with like" can be thought of as analogous to an attraction or affinity of a brood item with neighboring brood items, as if brood of the same type sticks together with a certain cohesion. To achieve concentric regions of sorted brood, it is necessary to make

one additional assumption. We assume that brood of the same type has an affinity for neighboring items of the same type as in the Deneubourg model, but in addition, there is a certain specified, but weaker affinity of a brood item for a neighboring brood item of a different type. This assumption is warranted on the basis of the observation that the ants maintain the brood in a coherent cluster rather than as a series of discrete islands of same type brood. This additional brood sorting rule is only a slight extension of the rule proposed in the Deneubourg model, and does not contradict any of the known behaviors of the ants. Although it was not specifically mentioned in Franks and Sendova-Franks (1992) as an aspect of the behavioral of the ants, it is unlikely to have been noticed at the level of analysis undertaken in their study. This assumption was also made because it is the basis of a proposed model of cell sorting in developmental biology (Steinberg 1963) that readily yields a concentric structure.

Relating self-organizing brood sorting in ants to a more general process of morphogenesis in developmental biology is the second reason for presenting this model. It is becoming apparent that self-organization approaches are not only crucial for understanding how collective intelligence emerges from the activities of thousands of individual colony members, but also for understanding biological organization in general. Furthermore developments in one field (such as morphogenesis) may provide insights into other fields.

I simulate the brood sorting process of ants on a 2-dimensional grid of uniform locations. Each grid location can either hold a single brood item or the location may be empty. For simplicity, as in the Deneubourg model, brood items are classified into only two types, eggs or larvae, rather than the 5 types distinguished by Franks and Sendova-Franks (1992). The simulation is initiated with a random array of a specified number of the two brood types. The remaining locations are empty. The simulation consists of a series of brood item movements on the grid. A brood item is chosen randomly but is picked up with a probability that is a function of the number of brood items immediately surrounding it. The brood item is then moved and has a greater probability of being set down the greater its affinity for its nearby neighbors. The measure of the affinity or goodness of fit of the selected brood item with its immediate neighbors is a weighted function of its immediate brood neighbors. In the Deneubourg model, the goodness of fit was assumed simply to be an unweighted function of the number of same type brood neighbors. That was the simplest and most logical assumption to make lacking any more detailed information. In this model I assume that there is a "cohesion" of eggs for eggs and larvae for larvae as in the Deneubourg model, but in addition I assume that there is also a measurable "adhesion" between dissimilar brood items. Furthermore, the value (weight) of each type of attraction is not equal. The relative affinity values are as follows egg:egg > egg:larva > larva:larva. (In contrast, in the Deneubourg model gives equal weight to each type of interaction: egg:egg = larva:larva.)

Thus the simulation consists of selecting more isolated brood items (with poor fit) and moving them to a new locations where they have a greater affinity to their neighbors. By simply giving different weights to each type of brood interaction, the model readily generates a concentric pattern resembling brood sorting by Leptothorax ants (Franks and Sendova-Franks, 1992).

What support is there for this model? Trinkaus (1969) discusses various theories of cell segregation in which a concentric pattern of cells develops from an initially random arrangement of 2 cell types. One test of the validity of a particular cell sorting hypothesis is to compare not only the final result of the hypothesized model (the pattern of cell segregation) but also to examine how the pattern develops over time. As seen in Trinkaus (1969, Fig. 7-5) different hypotheses of sorting yield different intermediate patterns. A prediction of a differential adhesion model such as that proposed here for brood sorting is that early in the sorting process islands of brood form, separated by empty spaces. These brood clusters show a tendency for the eggs to cluster within them. As the simulation progresses to the final fully-sorted stage, the clusters coalesce into a
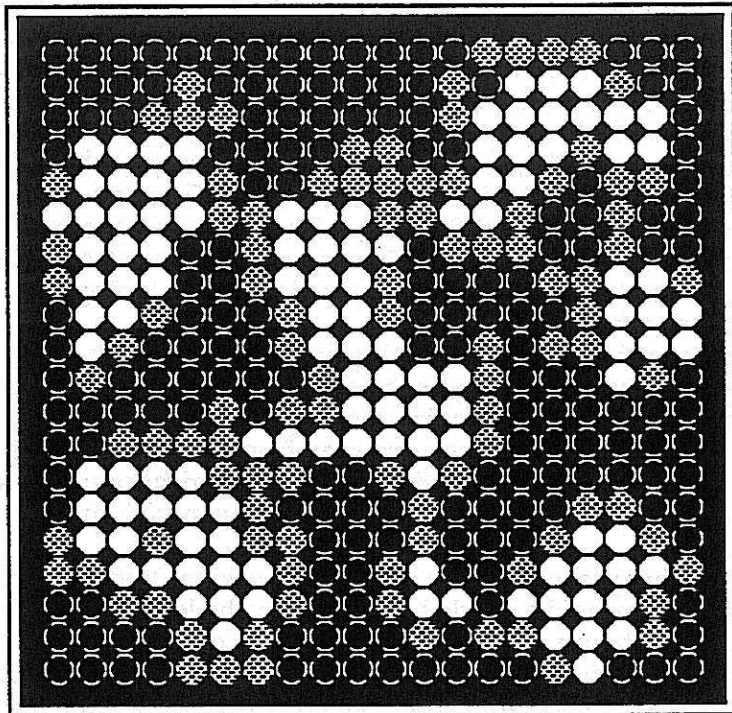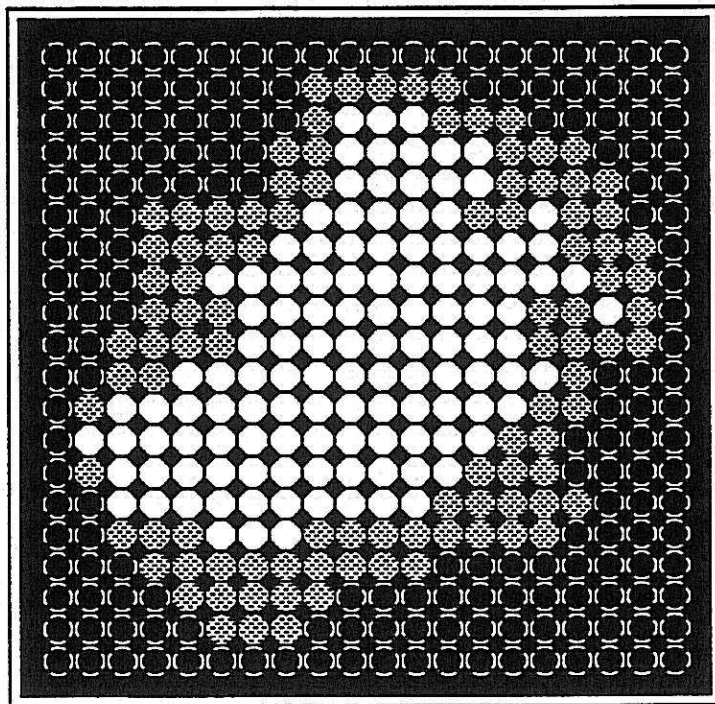
Figure 6a

Figure 6b

single brood cluster with eggs in the center. This pattern of development does not occur with the other mechanisms discussed but does occur in the model of brood sorting by ants. Figures 6a,b show the early and final stages in a brood sorting process governed by differential affinity. (Eggs are represented by white circles, larvae by gray, and empty locations by black).

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