

**SWARM INTELLIGENCE IN SOCIAL INSECTS AND THE EMERGENCE OF
CULTURAL SWARM PATTERNS**

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KEYWORDS / ABSTRACT : Swarm Intelligence / Self-organization / Social Insects / Collective Problem Solving / Artificial Life / Emergent functionality. This paper focuses on the reciprocal causality which exists between the organization of social insects' colonies (behavioral differentiation, spatio-temporal patterns of activities, collective decisions, ...) and the structuration of the environment as a consequence of the actions of the colony. This constitutes a basis to explore different kind of phenomena : how to achieve a collective task assignment without any centralized organizer; how a collective representation emerges at the level of the colony without any symbolic representation at the individual level; how to collectively build a complex architecture without blueprint. To characterize these collective behaviors in which a coherent functional global pattern emerges through simple local agents interacting with each other and with their local near environment we introduce the concept of Swarm Intelligence. Swarm Intelligence applies to animal or even artificial groups that exhibit intelligent behavior at a group level, mainly through achieving a distributed problem solving, well beyond that shown by its individual members. In swarms the structure of the social organization or the architecture of the nests produced is perpetuated from one generation to another. This creates a process that enables a collective structure to be transmitted without any true cultural tradition.

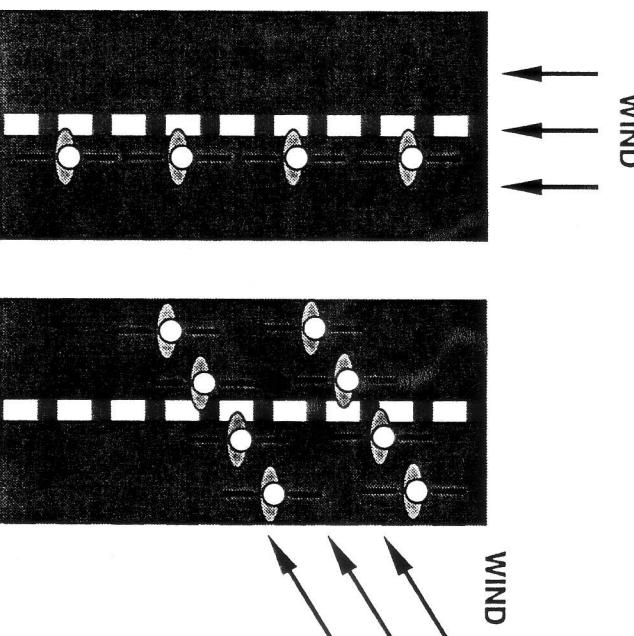


Figure 1. Exemple of field effect : the collective pattern of the squad in a cycle racing is a function of the direction of the wind.

For a long time insect's societies have been considered as a super-organism or a somewhat like a collective brain, but this metaphor loses the main characteristic of these societies. In fact, what is particularly striking is that its components are separated from each other and that each individual is mixed with the maternal components of the environment where it is moving about. It is a kind of brain having its cells mixed to the problem to solve. Then the society is able to sense, process and act on the information coming from the environment in which it is scattered but in a distributed way, both the perception and the action taking place at the individual level. This fact constitutes the essential property of the swarm activity which accounts for its specific behavioral, and architectural patterns. The collective performance results from the integration of the myriads

of individuals' activities, with each individual both processing information produced by the activities of others and stimulating and informing them in their turn. And for the observer "the whole behaves as a unit in the same way as if there was a coordinating agent "virtually" present in its center" (VARELA, 1991).

We would like to emphasize on the reciprocal causality that exists between the organization of the colony in its various aspects (behavioral differentiation, spatio-temporal patterns of activities, collective decisions, ...) and the structuration of the environment. This reciprocal causality is able to explain both the specific patterns of colonies' organization as well as the architectures that are build by the colony. This mutual process could have also affected the behavioral evolution in social insects in order to produce specific kind of organizations as well as specific kinds of architectures. Moreover, such a mutual process seems to be largely widespread. Indeed, we would like to point out that similar kinds of phenomena appear with human collective behaviors leading to specific patterns.

kind of pattern emerges either in a team in which all the individuals are cooperating together or in a group where every individual is running for himself. Indeed such a structure is able to emerge just as easily by "trials and errors." This structure can be obtained with the help of a learning process or the individuals can discover again the right position without any learning process. This kind of field effect that leads to specific structures can be seen in other situations. Thus, in BRITTANY, some villages spontaneously adopt an arrow-structure in order to minimize the effect of the wind (see GRILLOT, 1975). Some of these patterns are then frozen by the cultural process, and appear in some places where they lose their original functionality.

In order to characterize this kind of collective behavior in which a coherent functional global pattern emerges through simple local agents interacting with each other and with their local near environment, we have introduced the concept of *Swarm Intelligence* (THERAULAZ *et al.*, 1990b, THERAULAZ and GERVET, 1992). Swarm Intelligence applies to animal or even artificial groups that exhibit intelligent behavior at a group level well beyond that shown by its individual members. The dynamical organization of a social insect's colony is a striking example of this notion, whose efficiency is reflected in their widespread ecological success. It is now evident that a colony's collective performance depends as much on the interactions between the individuals and with their environment as on an individual complexity. In spite of the workers generally limited behavioral repertoire and learning capacity, and their inherently random character, the colony is a well-organized and stable structure that nevertheless responds adaptively to the unpredictable nature of its environment and changes in its internal composition due to births and deaths.

Section 1 defines some of the concepts of Swarm Intelligence, while section 2 presents various aspects of this distributed intelligence and focuses at each time on the role played by the reciprocal causality we introduced above in the genesis of specific patterns. Section 3 outlines the role played by the environment and tries to establish the distinction between true and false cultural swarm patterns.

2. Fundamentals of Swarm Intelligence

These last years, the interest in the adaptability of social systems in insects has been renewed (see DEBBIBOURG & GROSS, 1989 for an overview). Indeed, these non-linear systems can display a large variety of rich and even very complex behaviors, even though the constituent individual behavior is paradoxically very simple and has a strong random component. Local behavioral and environmental constraints and local information control the behavior of each individual. The resulting collective patterns characterize either the differentiation and spatio-temporal organization of the insects or the kind of structures which are produced. One particular approach is to analyze the performance of the social group as a form of collective problem solving. In this kind of analysis, the question is to determine what are the characteristics at the level of the different elements which govern the efficiency of the solving process and how the environmental factors regulate the form of the solution adopted by the colony. In order to do this, the studies combine a detailed biological analysis of individual behavior with numerical simulations to link this level with the colony's global behavior. The concepts we introduce thereafter are aiming to describe the phenomenology of the dynamical organization of swarms, as well as the formal causes of their collective behavior.

2.1. SWARM

We define a swarm as a set of (mobile) agents which are liable to communicate directly or indirectly (by acting on their local environment) with each other, and which collectively carry

out a distributed problem solving (THERAULAZ *et al.*, 1990b; THERAULAZ & GERVET, 1992). In this sense we prefer to *emergent functionality* (STEELS, 1990, 1991) or *functional self-organization* (AKON *et al.*, 1990), since this emerges from swarm's internal dynamics and its interaction with the environment. The swarm functioning induces both the genesis of functional collective patterns which characterize the differentiation and spatio-temporal organization of the agents of the swarm and the parallel organization of the material elements in the environment upon which each agent has an action. We will see that close connections exist between these different patterns and the specific categories of problem which are able to be solved by a swarm. Swarm intelligence can then be considered as a property of non-intelligent agents exhibiting collectively intelligent behavior.

2.2. PROBLEM AND COLLECTIVE PROBLEM SOLVING

In the framework of swarm functioning the concept of a problem can be defined as a kind of description of the position of a biological or artificial agent, where a functional outcome is described as a goal even though some parameters having the possibility to evolve with time are described as constraints. One can consider the problem to be set when the goal, the constraints and the lawful procedure to move from an initial state S_0 to a final state S_f taking into account the swarm and the environment in which the swarm is scattered. It is worth noting that this definition not only applies to a swarm but also to a single agent. The swarm is characterized by the collective resolution of the problem. Depending on whether an artificial or biological system is considered, the description of the problem to be solved will take a different look:

- when we consider an artificial system, the problem can be conceived before the design of the swarm whose local elementary behavioral rules will bring the system to solve this problem in a given environment ;
- but when we consider a biological system, the specification of the problem is equivalent to identifying a specific biological function (*e.g.* : the building behavior, the task assignment,...).

The solution of the problem can be considered in both cases as a particular state of the swarm environment system through which the functional outcome looked for is reached. As a rule, a number of solutions exist for a given problem, meaning that a given goal is compatible with several states of the system constituted by the swarm and its environment. Thus the "collective resolution of the problem" lies in the structural co-evolutionary process between the swarm and its environment in which the functional outcome described as a goal is reached.

Taking an ant hill as an example : observation shows different elements constituting the brood (eggs, larvae and pupae) are sorted and aggregated into piles of the same type by the workers (FRANKS, 1989 ; SENKOVA & FRANKS, in prep.). The sorting can be smaller and discriminate several larval instars. In this example the goal is sorting the different elements which constitutes the brood, the problem is how to achieve this ? The variation in the final number of aggregates we obtain : such as three (eggs, larvae, pupae), four (eggs, small larvae, big larvae, pupae) or more, represents different solutions to the problem. The resolution is the process by which the swarm reaches one of these solutions (see DEBBIBOURG *et al.*, 1990b, 1991 for further information about a particular example of sorting algorithm).

2.3. WHAT THE KINDS OF PROBLEMS CAN BE SOLVED BY A SWARM ?

Solving a problem with a swarm amounts to a morphogenetic process leading to a form which is the solution of the problem. Such a process involves both a structuring of the group of agents and the environment in which the swarm moves. If one specifies the different kind of problems a

swarm is able to solve, one identifies the elements this structuring process is acting on. Indeed, in a swarm, the structure of the environment and the organization of the group of agents molding each other. Both make up the double sides of the same structuring process. The problem to be solved may still turn on one face or the other : organizing the environment or specifying and organizing in space and time the individual activities of each agent.

Numerous studies have dealt with these two classes of problems. Problems such as task allocation, coordination, collecting material inspired by social insects or other social groups, can support similar discussions and speculations. Different examples of this decentralized and collective intelligence have been discussed, including: building behavior (DINETBORG, 1977; BRITTON *et al.*, 1986 ; SKARKA *et al.*, 1990), collective choice (PANTHES *et al.*, 1987 ; BICKERS *et al.*, 1990 ; SIEFFY *et al.*, 1991 ; CAMAZIN & SNEYD, 1991), the formation of trail networks (ARON *et al.*, 1990), sorting (CAMAZIN, 1991 ; CAMAZIN *et al.*, 1990 ; DINETBORG *et al.*, 1991), collective exploration (DINETBORG *et al.*, 1989 ; FRANKS, 1989 ; FRANKS *et al.*, 1991) and dynamical division of labor (DINETBORG *et al.*, 1987 ; CORBARA *et al.*, 1991 ; THIRAUTZ *et al.*, 1991b) synchronization and the generation of oscillations (FRANKS *et al.*, 1990 ; GOSS & DINETBORG, 1988 ; KRAFFT & PASQUIER, 1991). When the problem turns on the structuring of the environment, the swarm changes the structure characterizing a set of objects spread over the environment with handling operations. Different algorithms have been elaborated to enable an artificial swarm to sort different types of objects. The algorithm used by DINETBORG *et al.* was inspired from the processes used in ant colonies to sort their brood (DINETBORG *et al.*, 1990b, 1991). When we simulate a swarm of artificial ants with simple elementary and reshaping properties reproducing the behavior of ants, the swarm's activity is coordinated and we obtain the sorting of two or more classes of objects. But the problem may also turn on the structuring of the behavioral units of the swarm to realize a spatio-temporal distribution (BICKERS *et al.*, 1990 ; DINETBORG *et al.*, 1989, 1990a ; FRANKS *et al.*, 1989) or a functional specialization in the agents' activities (THERAULAZ *et al.*, 1990a, 1990b, 1991a, 1991b).

3. Embodiments of Swarm Dynamics

We shall now examine several examples of swarm dynamics in which the reciprocal interaction between the structure of the colony and the organization of the environment accounts for the specific patterns produced. To do this, we examine three self organizing models with each one focusing on a particular aspect of swarm's activity.

3.1. A COLLECTIVE TASK ASSIGNMENT WITHOUT ANY CENTRALIZED ORGANIZER

Division of labor occurs in many eusocial insects' societies. At each time, all the individuals of the colony must perform a certain number of tasks which varies in space and time and which depends on the internal needs of the colony as well as on the particular environmental conditions. Then the question is : how the colony is able to allocate the tasks to be done and to coordinate the activities of each individual. In other words, how is it possible to relate local individual interactions, their effect onto the individuals in which they occur and how on this basis is it possible to explain the organization of the great behavioral forms which appears in the colony. This occurs in particular in a primivately eusocial wasp species called *Polybia dominula* Christ (THIRAUTZ *et al.*, 1991a). These wasps have little differentiation and no morphological differences between castes or predetermined control of activities depending on age or on any other known physiological predetermined. Here again, the integration of the individuals' activity depends essentially on the interactions occurring between the colony members and with their immediate environment.

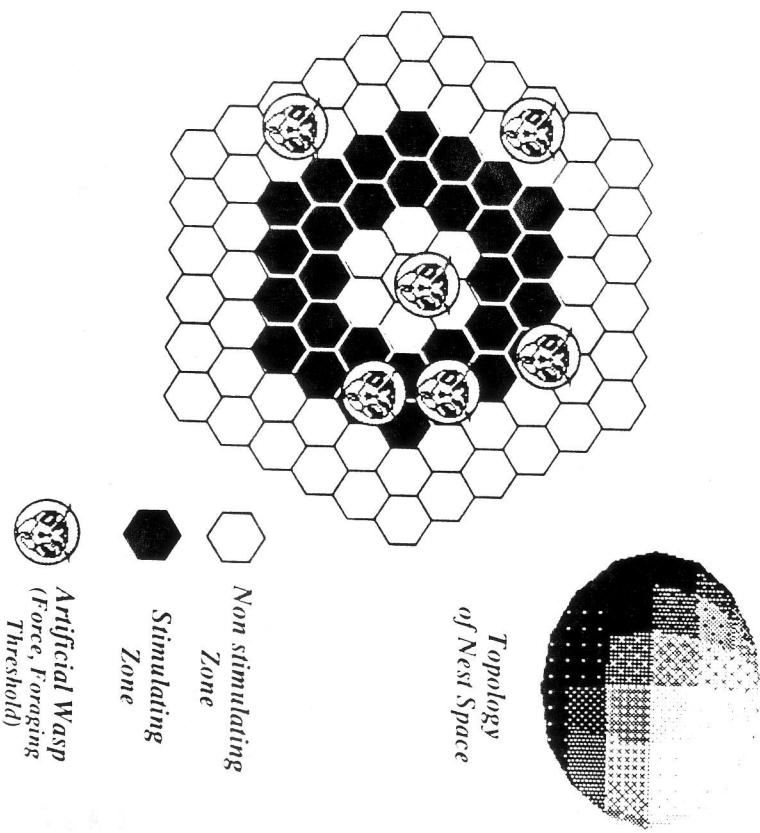


Figure 2. Structuration of the nest space

A double morphogenetic process occurs. First, each individual acquires its own behavioral profile, related to the different tasks in and outside the nest. Second, the ensemble of these profiles constitutes the way in which the colony has divided the different tasks to be performed amongst the different members. In the colonies, one can distinguish three main tasks: egg laying (tasks performed by just one individual - the queen or the α individual), foraging and brood care, and finally doing nothing. The individuals involved in this latter "task" constitute a sort of reserve labor pool that can be more or less mobilized in response to the overall work load. Furthermore, each of these three tasks is oriented towards a different part of the nest: the egg layer remains in a zone where there are cells ready to receive eggs, the foragers/brood carers activity is concentrated towards zones occupied by the larvae, and the inactive wasps are found at the edge and the back of the nest.

Traditional approach has been to consider the queen or the α -individual as the main central organizer of the colony through changes of its own level of activity. However, the implementation of the interactions which control the individual behavior and the simulation of artificial colonies reveals that the task assignment, the parallel spatial distribution process and the hierarchical organization of the colony emerge out the interactions occurring both between individuals and with their environment. Two types of interactions control individual behavior in *Polistes dominulus* Christ wasp colonies. A hierarchical type of interaction which appears in dominance scenes. When two wasps meet, they carry out a ritualized fight in which one wins (the dominant) and the other loses and is pushed toward the edge of the nest (the subordinate). The more subordinate the individual is, the less likely it is to show dominance behavior. Moreover, the higher the probability that an individual will dominate in a hierarchical interaction, the greater its propensity will be to frequently dominates its subordinates. In this way, each wasp reinforces its probability of dominating through the number of times it is successful in hierarchical interactions and each subordination has the opposite effect. These relationships extend throughout the society as a whole and organize it along a linear hierarchy. The second type of interaction is a trophic type which controls the relationships between the individuals and the environment, particularly with the brood, which in turn triggers some types of activities towards the brood, such as brood-tending and/or collecting prey and the subsequent feeding of larvae. Each individual is characterized by differential reactivity threshold to the various brood components (the eggs, small and large larvae and pupae), which may evolve along the time in function of the individual's activity. In fact, there is a parallel self-facilitating process which causes the increase in the amount of time spent foraging by individuals which have already foraged previously (THIBAULAZ et al., 1991a).

3.1.1. The elementary behavioral rules. In the model each wasp is represented by a unit having the ability to interact both with similar units and with some characteristics of the environment. The model describes the activity of n wasps, whose number remains constant with time where dominance-subordination exist, and integrates two local action rules. Each individual is characterized by two variables, the force F which intervenes during random encounters within the nest, and by a response threshold σ to larval stimulations located in a specific zone of the brood (see figure 2). At the beginning of the simulation, the n individuals of the colony are identical. The behavioral forms which characterize the colony are then generated by the combined action of two autocatalytic processes (dominance and foraging). The force value of each individual varies with each combat. Every time it wins or loses its force F increases or decreases along with an intrinsic coefficient of reinforcement which is common to all the individuals. Moreover its probability of winning or losing is a function of its own and rival force. Thus each time a wasp wins it increases its force and its probability of winning its next combat. This positive feedback rapidly separates a group of initially equal wasps into a dominance hierarchy with dominants (high force individuals) and subordinates (low force ones). The foraging threshold evolves along a similar process. There is again a positive feedback mechanism, since each time a wasp forage it increases its probability of foraging, and each time it doesn't it decreases its probability of foraging the next time. Again this can rapidly separate a group of initially identical wasps into two subgroups of foragers and non-foragers.

3.1.2. The colony' behavioral patterns. The system is characterized by one or more stable configurations (or attractors) corresponding to the force, foraging threshold and average position of the initially equals individuals. For a given set of parameters values, the system spontaneously evolves towards one of these configurations. But one cannot what any particular individual history will be. Figure 3 presents a simulation of a colony of 8 individuals. Three behavioral categories of individuals are generated which correspond exactly to those appearing in real

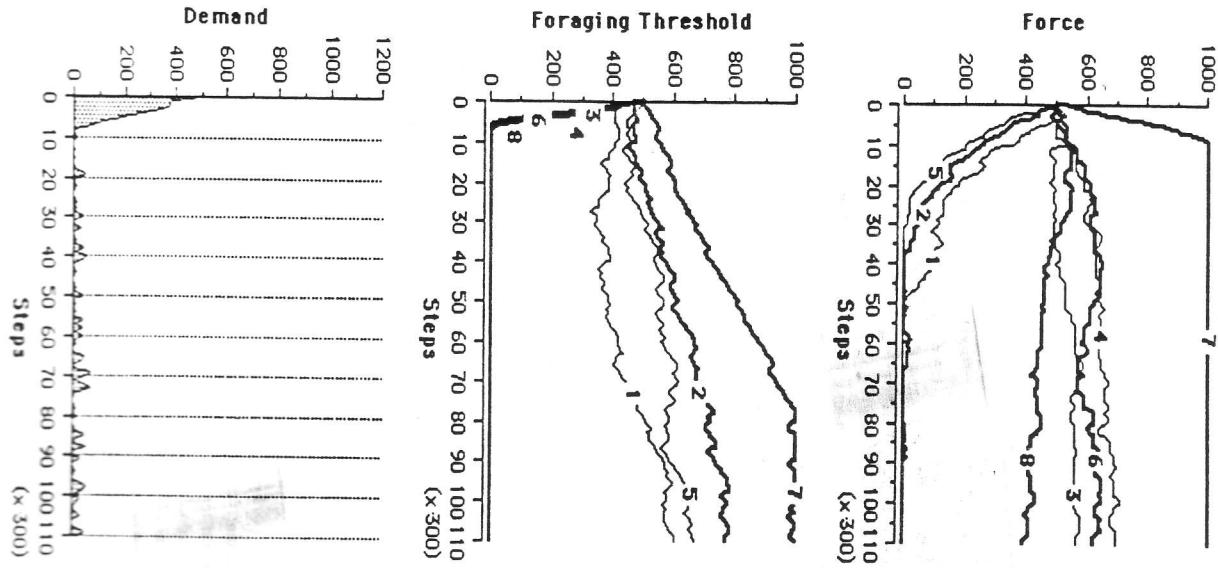


Figure 3. Collective behavioral organization in a wasp nest. The model describes the parallel evolution of the behavioral variables (Force and Foraging Threshold) in a colony of 8 individuals. For each individual the coefficient of reinforcement of the force and the foraging threshold is 10, and the foraging coefficient for the foraging is 0.03.

colonies. The first behavioral form corresponds to a unique individual, whose force increases rapidly to a maximum, and whose foraging threshold increases to a maximum. This alpha-individual therefore remains on the nest, involved in many encounters and always dominates the others. The second behavioral form characterizes a group of individuals whose foraging threshold rapidly decreases to a minimum. They are the active foragers who control the level of the brood 'hunger' which drops to fluctuate around a low level as they take up their foraging role and bring food. As they are often outside the nest they can maintain an intermediate level of force. And the last behavioral form characterizes individuals with intermediate or high foraging threshold. So they forage occasionally, remain most of the time on the back of the nest, they are frequently dominated and have a low force.

Here we can see that the collective pattern that is generated reflects the coupling between the structuration of the nest space and the elementary behavioral rule which characterize the individuals. The group function is generated by a double feedback system controlling individual behavior : Positive feedback rapidly amplify small random fluctuations among the competing wasps and have morphogenetic effects. In the case of the force value, direct competition among individuals leads to the hyperactivity of a single wasp up to the biologically possible limit. The more indirect nature of the competitive interactions between the wasps explains why the number of foragers can vary as a function of the intensity of the larval demand and the foraging time. The cyclical relationship which exists between brood satisfaction and foraging activity maintains a regular level of social demand which regulates the number of foragers (*i.e.* the wasps which have a minimum foraging threshold). Moreover, the structuration of the nest space accounts for the spatial distribution of the three behavioral groups of wasps.

3.2. A COLLECTIVE REPRESENTATION WITH REPRESENTATIONLESS INDIVIDUALS

One of the main features of the communications used by social insects in order to self-organise is randomness and positive feed-back. A standard example is given by food recruitment in ant colonies (see figure 4). When a new food source is discovered by an ant, it lays down a transient chemical trail. This pheromonal marking promotes in an indirect manner the other ants of the colony to follow this trail towards the place where the food was discovered. These ants, after feeding at the source, will reinforce the trail when they return to the nest. In so doing they themselves change from recruits to recruiters. This kind of communication enables the amplification of a discovery but also the selection of an information through the competition which might exist between several discoveries. Indeed, with the help of this autocatalytic logic and the use of spatial constraints, the strength of the "near source" signal increases faster than the strength of the "far source" signal. The latter will be eliminated afterwards. In this way a food source close to the nest will be selected more rapidly than a food source far away from the nest. This collective response of the society, showing in this special case a temporal structuring of the individuals' activity, is the solution to the problem in hand : in this example the exploitation of the closest food-source.

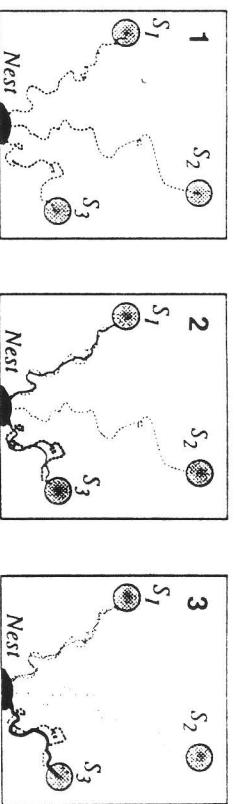


Figure 4. The exploitation of the closest food source shows how small random fluctuations can be amplified by the colony. S_1 , S_2 and S_3 are the food sources ; the thickness of the curves is a function of the stream of individuals following the trail.

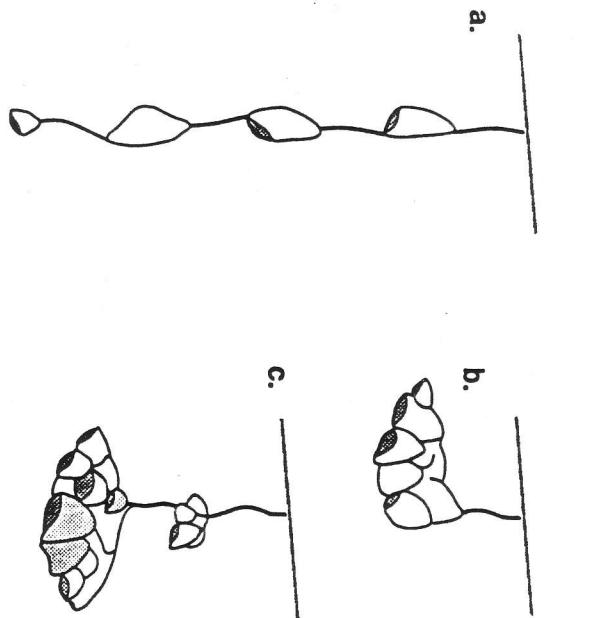
Through this example we put in place all the elements which give the collective problem solving in insect societies its original features. Even though none of the individuals in the colony is informed of all the possible ways to find a solution, and none have an explicitly preprogrammed solution, the colony as a whole converges towards an adaptive solution. We can thus see that without any particular spatial coding, the colony solves the problem using only an autocatalytic logic and the geometrical and physical constraints of the environment in which it moves.

3.3. A COLLECTIVE CONSTRUCTION WITHOUT BLUEPRINT : ARCHITECTURES WITHOUT ARCHITECTS

One question that has been for a long time set is about the way the insects collectively produced their nest architecture. Here again it seems that something like a blueprint is embedded somewhere in the brain of each insect. Indeed, as we shall see the architecture of the nests reflect the dynamics of the local behavioral interactions between the insects and their near environment. Figure 5 shows some aspects of the great diversity of nest architecture we observe in wasps. The variation of nest design extends from one cell per comb with an elongate form (a) to larger single combs (b) and multiple stacked combs with a varying number of cells per comb (c). Combs are suspended either to the substrate or from the rim of the cells of the upper comb. Then the question is : why do these structures have the form they have ? To answer this question we build a model in which the environment is a lattice divided in $n \times m$ cells which can be empty (0) or full (1). Moreover the behavior of each wasp is idealized with local behavioral rules.

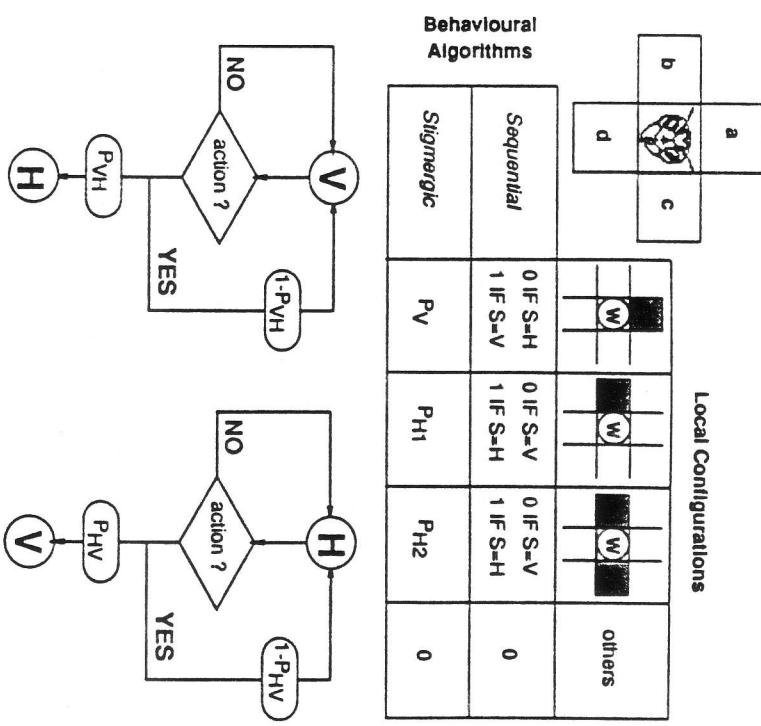
3.3.1. The elementary behavioral rules. Two types of behavioral rules can be tested. The first which is called stigmergy is inspired by different biological observations. Our first goal with such a model is to examine the power and the limit of given rules, rather than to fit theoretical and experimental results. GRASSE introduced the concept of stigmergy in 1959 to explain the collective genesis of the termites' nest (GRASSE, 1959). The basic idea is that no direct interactions are necessary to coordinate the work of a group, but that the interactions between the nest and the workers are enough. The working termites modify their environment, providing new stimuli. These new stimuli induce new behavioral responses which in their turn modify the environment. With this succession of stimulus-reaction, the society is able to produce a structure.

Figure 5. Some aspects of the diversity of wasp nest architecture. The following genera and species are representative of the nest types shown : a. *Mischocyttarus punctatus*, b. *Polybia*, c. *Stenogastrinae*, *Parachilogaster melleji*. Redrawn from HANSELL 1984 and JEANNE 1975.



It is the work itself which assumes the coordination of the workers' activities. So in the stigmergetic algorithm, only the local configuration met by the wasp determines its behavior, which is here reduced to fill or not the corresponding cells. The local configurations are the first four neighbors cells which surround the cell occupied by the wasp. From the 16 possible configurations, only three configurations stimulate the filling of the cell (see figure 6). Two correspond to the horizontal mode and one to a vertical mode. Each mode is characterized by a probability P_{H1} , P_{H2} and P_V of filling the corresponding cell met by the wasp. The second type of algorithms we tested is called sequential. In this case, the past activities of a wasp affect its building activity. The local configuration does not play a stimulating role, but only authorizes the wasp to fill, or not, the cell. It is the state of the wasp which controls its activity. At time t the wasp can be in the state "horizontal" or "vertical filling". The wasp in the state horizontal (vertical) can only fill a cell in the configuration "horizontal filling" ("vertical filling"). Having exhibited a vertical (horizontal) filling, the animal has a probability P_{VH} (P_{HV}) of becoming an horizontal (vertical) builder. The wasps move randomly on the nest and in its neighborhood.

Figure 6. Definition of the behavioral algorithms used by artificial wasps.



3.3.2. *The colony' behavioral patterns*. Comparing the rate of building per insect for different colony sizes, the sequential algorithm shows an increase of efficiency. The stigmergetic mechanism generally shows an increase as in the digging model. Moreover, the form produced is much more stable (the same form is almost always produced) in the sequential case than in the stigmergetic one (see figure 7). When the number of agents is increasing, the stigmergetic algorithm produces forms that are more "complex", in terms of mutual information between the states of two neighboring cells, than the form produced by the sequential algorithm. This model shows that the sequential program seems to be more adapted to a solitary individual or a small group than to large numbers. The analysis of the architecture of wasps' nest shows that their complexity increases with the transition from solitary to social life. We can see that one way to reach this complexity is to shift from a sequential to a stigmergetic behavioral algorithm. One interesting question which still remains is : what could be the functionality of such an increase ?

Stigmergic algorithm

Sequential algorithm

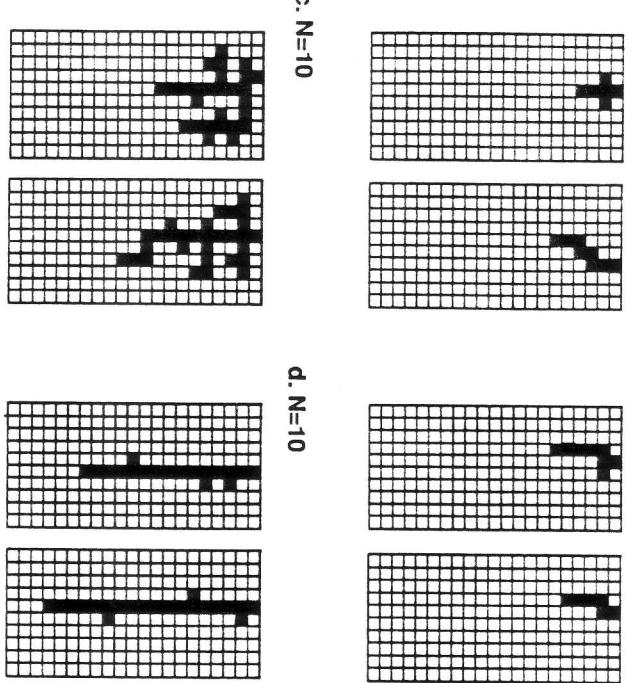


Figure 7. Architectural patterns obtained in a 2-dimension world with the stigmergic and the sequential algorithms. a. Solitary insect ($N=1$), stigmergic algorithm, $P_V = 0.8$; $P_{H1} = 0.2$, $P_{H2} = 0.4$. b. solitary insect ($N=1$), sequential algorithm, $P_{VH} = 0.2$; $P_{HV} = 0.8$. c. Idem as a), but the structure is obtained with $N=10$ individuals. d. Idem as b), but the structure is obtained with $N=10$ individuals.

4. Discussion.

4.1. THE ENVIRONMENT AS A MAP-MEMORY.

We have seen that two processes gave its identity to the swarm functioning : the random movements of the individuals and positive feedback mechanisms which strongly interact with the geometrical and topological constraints of the environment to give its own characteristics to the swarm patterns. The fundamental logic is then given by the interplay that exist between multiple random perceptions and actions and their consequences on both the individual behavior and the structure of the environment. Each action changes the landscape in a way that affect the resulting

behavior of the colony. Small random fluctuations affect some environmental variables as the result of random activities of the insects. These random fluctuations (e.g.: the decrease of larval demand in the area occupied by the brood in the wasp nest, the creation of a seed in the building behavior, etc...) will then affect the behavior of the insects in the colony, which results in a decrease of the randomness. As a result of their past action the behavior of the insects is modified; sometime the spatio-temporal activity is only affected through changes in the environment; sometimes it affected the probability to do a particular action on the environment through learning processes. In other words the swarm self-organizes through its own produced distributed activity. One could say that the environment is playing the role of a spatio-temporal memory which selects and directs the present action of the swarm.

It is worth noting that the swarm functioning does not imply any global representation or planning of the task to be doing, nor coded representation of the environment in a map form. Indeed, nor their processing abilities nor the properties of the signal they perceived enable the individuals to elaborate a global representation of their environment and to plan their actions. The indirect interactions that are resulting from the actions of the individuals on the environment replace the plan of action. They produce a kind of "landmarks" in the environment which evolve in space and time. It is no more necessary that a "map" exists at the level of the swarm. The directional data are directly picked up in true-size at the level of the environment. One could say that the environment is playing the role of a full-sale model.

4.2. TRUE AND FAKE CULTURAL TRADITIONS IN SWARM DYNAMICS.

In social insects' societies an interesting phenomenon is occurring. Indeed it seems that something like a culture appears at the level of the swarm. Indeed, we saw that the swarm can be characterized by collective structures and nest architectures. So it seems to be the form (social organization and artifacts produced) which is perpetuated from one generation to another generation. But we cannot so to speak use the term of cultural tradition since there is no culture at the individual level. Indeed if we transpose an individual from a colony A to a colony B it will not be able to transmit the features of its own social organization. This is not surprising since we saw that these specific patterns results from the interactions between the individuals and generally speaking from the group functioning. Thus some processes allow for the perpetuation of a structure without requiring any cultural transmission. In insects societies (and in other groups) we find numerous examples of permanent behavior at the group's level which are interpreted as a cultural effect (transmission and learning) or the identical response of individuals to environmental cues. However a number of examples can not be explained with such hypothesis and are much more fake tradition randomly selected. When very strong mass effects exist inside a group, the new arrivals are obliged to adopt the same behavior as others. Chemical trails in ants are a good example. The new ants which "discover" a trail for the first time, follows this trail and reinforce it. The trail is like an external and collective memory. Its form depends of its history and is able to perpetuate on long time, and this without individual memory. However the trails can be also the touchstone of "cultural phenomena" in ants.

In order to get such a true cultural tradition, there must be a behavioral acquisition and the transmission of this one at the individual level. We can find such processes where the communication and the transmission of an information occur. One of the best example of such a true cultural tradition is that of "trunk-trails" in ants (the classical example is the genus *Formica*, Rosengren 1971). These trails remain stable from year to year, and the ants follow the same path before and after the winter which is a period of inactivity for the colony. When ants discovered a food source they recruited with laying a trail as we saw in section 3.2. This trail attracted native ants which became specialists to the trail after n trip. When winter arrived the trails are erased. In spring, the old ants remembered the path (this process implies a visual memory) and re-traced the

trail. This one will guide the young ants and the system is perpetuated in this way. With this phenomenon one is faced with numerous questions. In particular one could be interested by the reliability of the individuals' memory and the extent of the amplification phenomena through the trail if we refer to the size and the life of the food source. Indeed if the learning process at the individual level is too strong or the memory too high, then the colony may be trapped into a non-optimal solution. This will appear when the landscape changes and the food sources disappear. Thus it is important to maintain a certain level of plasticity which can be randomness and forgetting at the individual level, in order to discover new food sources and allow different kind of organizations. In this way the individual behavioral strategy is better adapted to the evolving structure of the environment, what we have seen with studying swam dynamics.

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