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The biological principles of swarm intelligence

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Abstract The roots of swarm intelligence are deeply embedded in the biological study of self-organized behaviors in social insects. From the routing of traffic in telecommunication networks to the design of control algorithms for groups of autonomous robots, the collective behaviors of these animals have inspired many of the foundational works in this emerging research field. For the first issue of this journal dedicated to swarm intelligence, we review the main biological principles that underlie the organization of insects' colonies. We begin with some reminders about the decentralized nature of such systems and we describe the underlying mechanisms of complex collective behaviors of social insects, from the concept of stigmergy to the theory of self-organization in biological systems. We emphasize in particular the role of interactions and the importance of bifurcations that appear in the collective output of the colony when some of the system's parameters change. We then propose to categorize the collective behaviors displayed by insect colonies according to four functions that emerge at the level of the colony and that organize its global behavior. Finally, we address the role of modulations of individual behaviors by disturbances (either environmental or internal to the colony) in the overall flexibility of insect colonies. We conclude that future studies about self-organized biological behaviors should investigate such modulations to better understand how insect colonies adapt to uncertain worlds.

Keywords Swarm intelligence · Social insects · Stigmergy · Self-organization collective behaviors

1 Introduction

Swarm intelligence, as a scientific discipline including research fields such as swarm optimization or distributed control in collective robotics, was born from biological insights about the incredible abilities of social insects to solve their everyday-life problems (Bonabeau

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et al. 1999). Their colonies ranging from a few animals to millions of individuals, display fascinating behaviors that combine efficiency with both flexibility and robustness (Camazine et al. 2001). From the traffic management on a foraging network (Burd 2006; Couzin and Franks 2003; Dussutour et al. 2004; Vittori et al. 2006), to the building of efficient structures (Buhl et al. 2004, 2005; Theraulaz et al. 2003; Tschinkel, 2003, 2004), along with the dynamic task allocation between workers (Beshers and Fewell 2001; Bonabeau et al. 1998; Deneubourg et al. 1987; Gordon 1996), examples of complex and sophisticated behaviors are numerous and diverse among social insects (Bonabeau et al. 1997; Camazine et al. 2001; Detrain and Deneubourg 2006).

For example, in their moving phase, the neotropical army ants *Eciton burchelli* may organize large hunting raids which may contain more than 200 000 workers collecting thousands of prey, be 15 m or more wide and sweep over an area of more than 1500 m^2 in a single day (Franks 1989; Franks and Fletcher 1983; Hölldobler and Wilson 1990). As another example, African termites of the species *Macrotermes bellicosus* build mounds that may reach a diameter of 30 m and a height of 6 m (Grassé 1984). These biological skyscrapers result from the work of millions of tiny (1–2 mm long) and completely blind individuals. Even more fascinating than the size of these mounds is their internal structure. Nests of the species *Apicotermes lamani* are probably one of the most complex structures ever built in the animal kingdom (Desneux 1956, see Fig. 1(a)). Over the outside surface of the nest, there exists a whole set of micro structures that ensure air conditioning and gas exchanges with the outside environment. Inside these nests, that are about 20 to 40 centimeters high, we find a succession of chambers connected together with helical ramps. These helical ramps arise from the twisting and soldering of successive floors. There are several stairs at each floor and some of these stairs go through the whole nest. Even distant chambers are in connection through these shortcuts.

Surprisingly, the complexity of these collective behaviors and structures does not reflect at all the relative simplicity of the individual behaviors of an insect. Of course, insects are elaborated “machines”, with the ability to modulate their behavior on the basis of the processing of many sensory inputs (Menzel and Giurfa 2001; Detrain and Deneubourg 2006). Nevertheless, as pointed out by Seeley (2002), the complexity of an individual insect in terms of cognitive or communicational abilities may be high in an absolute sense, while remaining not sufficient to effectively supervise a large system and to explain the complexity of all the behaviors at the colony scale. In most cases, a single insect is not able to find by itself an efficient solution to a colony problem, while the society to which it belongs finds “as a whole” a solution very easily (Camazine et al. 2001).

Behind this “organization without an organizer” are several hidden mechanisms which enable insect societies, whose members only deal with partial and noisy information about their environment, to cope with uncertain situations and to find solutions to complex problems. The present paper aims at reviewing these mechanisms that are by now a stimulating source of inspiration, especially when it comes to design distributed optimization algorithms in computer science or control algorithms in collective robotics (Bonabeau and Theraulaz 2000). Implementations in artificial systems of this swarm intelligence logic are nowadays numerous: discrete optimization (Dorigo et al. 1996, 1999), graph partitioning (Kuntz et al. 1999), task allocation (Campos et al. 2000; Krieger et al. 2000), object clustering and sorting (Melhuish et al. 2001; Wilson et al. 2004), collective decision making (Garnier et al. 2005), and so on.

All these examples rely on mechanisms known to occur in social insects. However, if social insects remain the original source of inspiration for artificial swarm intelligent systems it is important to notice that other biological systems share similar collective properties

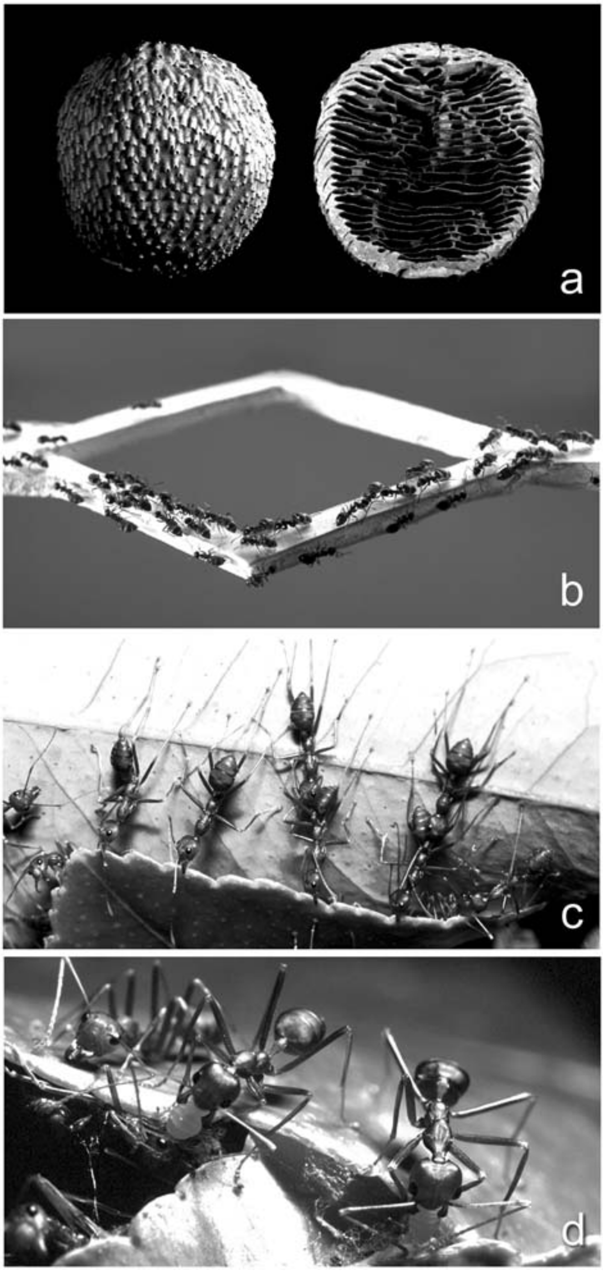

Fig. 1 Classification of collective behaviors in social insects. **a** An external view and a cross section of an *Apicotermes lamani* nest resulting from the *coordination* of workers building activities. **b** *Collective selection* of one foraging path over a diamond-shaped bridge leading to a food source by workers in the ant *Lasius niger*. **c** Weaver ant (*Oecophylla longinoda*) workers *cooperate* to form chains of their own bodies, allowing them to cross wide gaps and pull leaves together. **d** An example of *division of labor* among weaver ant workers (*Oecophylla longinoda*). When the leaves have been put in place by a first group of workers, both edges are connected with a thread of silk emitted by mature larvae held by a second group of workers. © CNRS Photothèque Gilles Vidal and Guy Theraulaz

such as colonies of bacteria or amoeba (Ben-Jacob et al. 1994, 2000), fish schools (Grünbaum et al. 2005; Parrish et al. 2002), bird flocks (Reynolds 1987), sheep herds (Gautrais et al. 2007) or even crowds of human beings (Helbing et al. 2001). Among them, the motions of fish schools and bird flocks have for instance partly inspired the concept of particle swarm optimization (Kennedy and Eberhart 1995). Nevertheless, we will restrict this review to collective behaviors of social insects for at least two reasons: (1) they represent the largest research corpus from both a theoretical and an experimental point of view; (2) their underlying principles are very close to those found or hypothesized in other animal species.

In this paper, we first describe in an historical perspective the basic mechanisms that explain the amazing collective abilities of insect societies. This part is illustrated with well-known examples and introduces the major concepts underlying the swarm intelligence research field: decentralization, stigmergy, self-organization, emergence, positive and negative feedbacks, fluctuations, bifurcations. It also highlights the nature of the relation between the behavior of the individual and the behavior of the group, an idea of great importance for understanding the third part of the paper.

In a second part, we introduce a categorization of these collective behaviors. This categorization is based on the interplay of four components that emerge at the level of the group from the interactions and behaviors of the insects. We name these four components: coordination, cooperation, deliberation and collaboration. We illustrate their role in the organization of a colony's activities through various examples taken from the literature published over the last 40 years.

The third part is dedicated to a problem which is central to swarm intelligence: the adaptation of the group to changes in the environment or in the composition of the group itself. We argue that this adaptation can be the result of an active modulation of individual insects' behaviors. In support of this argumentation, we provide three examples that cover three different kinds of swarm intelligent problem solving: division of labor, morphogenesis and collective decisions. We show in each case how small behavioral modifications participate to the overall adaptation of the colony to changeable life conditions.

Finally, the last part opens a discussion about the need to better understand the role of individual behavioral modulations in relation with the diversity of collective structures that a colony of insects is able to produce. It also provides some keys that could inspire further developments in the swarm intelligence research field.

2 The underlying mechanisms of complex collective behaviors

For a long time, the collective behavior of social insects has remained a fascinating issue for naturalists. Everything happens as if there was some mysterious virtual agent inside the colony that would coordinate the individuals' activities. Even today, success novelists like Michael Crichton have revived the old idea of the spirit of the hive (which was originally introduced by the Belgian poet Maurice Maeterlinck 1927); in his novel "Prey", Crichton describes a swarm of artificial insect-like nanorobots which is governed by such a collective mind, allowing them to take complex decisions and even to anticipate future events (Crichton 2002). Of course, we know that there is no such spirit in the hive. Reality is less trivial, and also much more interesting.

The quest for the mechanisms underlying insects' collective behaviors started more than a century ago and the first hypothesis put forward were clearly anthropomorphic (see for instance Büchner 1881; Forel 1921). Individual insects were assumed to possess something like a representation of the global structure to be produced and then they were supposed to use that representation to make appropriate decisions (see, for instance, Thorpe 1963). In other words, people were thinking that there was some direct causal relationship between the complexity of the decisions and patterns observed at the colony level and the behavioral and cognitive complexity that was supposed to be required at the individual level to produce these decisions and patterns. In particular, the queen was supposed to gather and monitor all the information coming from its colony and then supervise the work done by the workers, giving them appropriate orders. For instance, Reeve and Gamboa (1983, 1987) have argued that in colonies of the paper wasp *Polistes fuscatus* the queen functions as a central pacemaker and coordinator of workers activities. However, recent findings by (Jha et al. 2006) demonstrated that indeed this original statement was wrong. The kind of organization that was supposed to rule the society was hierarchical and centralized.

Nevertheless, most of the works that have been done in the last 40 years revealed a completely different organization (Theraulaz et al. 1998a). We now know that individual insects do not need any representation, any map or explicit knowledge of the global structure they produce. A single insect is not able to assess a global situation, to centralize information about the state of its entire colony and then to control the tasks to be done by the other workers. There is no supervisor in these colonies.

A social insect colony is rather like a decentralized system made of autonomous units that are distributed in the environment and that may be described as following simple probabilistic stimulus-response behaviors (Deneubourg et al. 1983). The rules that govern interactions among insects are executed on the basis of local information that is without knowledge of the global pattern. Each insect is following a small set of behavioral rules. For instance, in ants each individual is able to perform 20 different elementary behaviors on average (Wilson 1971). Organization emerges at the colony level from the interactions that take place among individuals exhibiting these simple behaviors. These interactions ensure the propagation of information through the colony and they also organize the activity of each individual. Thanks to these sophisticated interaction networks, social insects can solve a whole range of problems and respond to external challenges in a very flexible and robust way.

2.1 Stigmergy

The first serious theoretical explanation to the organization of social insects' activities was provided 40 years ago by French biologist Pierre-Paul Grassé, who introduced the concept of stigmergy to explain building activity in termites (Grassé 1959; see Theraulaz and Bonabeau 1999 for an historical review). Grassé showed that the coordination and the regulation of building activities do not depend on the workers themselves, but are mainly achieved by the nest structure. In other words, information coming from the local environment and the work in progress can guide individual activity. For instance, each time a worker performs a building action, the shape of the local configuration that triggered this action is changed. The new configuration will then influence other specific actions from the worker or potentially from any other workers in the colony. This process leads to an almost perfect coordination of the collective work and may give us the impression that the colony is following a well-defined plan.

A good example of stigmergic behavior is provided by nest building in social wasps. The vast majority of wasp nests are built with wood pulp and plant fibers that are chewed and cemented together with oral secretions (Wenzel 1991). The resulting paper is then shaped by the wasps to build the various parts of the nest: the pedicel, which is a stalk-like structure connecting the comb to the substrate, the cells or the external envelope.

Building activities are driven by the local configuration of cells detected by the wasps on the nest (Karsai and Theraulaz 1995). Indeed, the architecture by itself provides enough information and constraints to ensure the coordination of the wasp building activity. To decide where to build a new cell, wasps use the information provided by the local arrangement of cells on the outer circumference of the comb. They perceive these configurations of cells with their antennae. Potential building sites on the comb do not have the same probability to be chosen by wasps when they start to build a new cell. Wasps have a greater probability

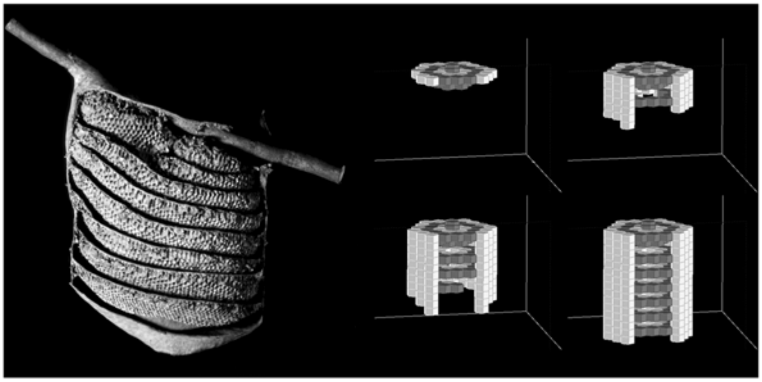

Fig. 2 A model of stigmergic nest construction in wasps. Simulation of collective building on a 3D hexagonal lattice (*right*). This architecture is reminiscent of natural *Chartergus* wasp nests (*left*) and exhibits a similar design. A portion of the external envelope has been partly removed to show the internal structure of the nest

to add new cells to a corner area where three adjacent walls are already present, while the probability to start a new row, by adding a cell on the side of an existing row, is very low (Camazine et al. 2001).

The consequences of applying these local rules on the development of the comb and its resulting shape can be studied thanks to a model in which wasps are represented by agents (Theraulaz and Bonabeau, 1995a, 1995b). These virtual wasps are asynchronous automata that move in a three-dimensional discrete hexagonal space, and that behave locally in space and time on a probabilistic stimulus-response basis. They only have a local perception of their environment where a virtual wasp perceives the first twenty six neighboring cells that are adjacent to the cell she occupies at a given time, and of course, this virtual wasp does not have any representation of the global architecture she is supposed to build.

Each of these virtual wasps uses a set of construction rules. As they move in space, they will sometimes come into contact with the nest structure and at this moment they will perceive a local configuration of cells. Some of these configurations will trigger a building action, and as a consequence, a new cell will be added to the comb at the particular place that was occupied by the wasp. In all the other cases no particular building action will take place and the wasp will just move toward another place. These construction rules are probabilistic, so it is possible to use in the model the probability values associated with each particular configuration of cells that have been measured in the experiments with the real wasps.

Nest architectures obtained by simulations show that the complexity of the structures that are built by social insects does not require sophisticated individual behavioral rules (see Fig. 2).

2.2 From stigmergy to self-organization: path selection in ant colonies

Another example of stigmergic behavior is food recruitment in ants (Hölldobler and Wilson 1990). Ants communicate with each other through the use of pheromones. These pheromones are chemical substances that attract other ants. For instance, once an ant has found a food source, she quickly comes back to the nest and lays down a pheromone trail. This trail will then guide other workers from the nest toward the food source. When the recruited ants come back to the nest, they lay down their own pheromone on the trail and reinforce the pathway. The trail formation therefore results from a positive feedback: the more ants use a trail, the more attractive the trail becomes. Of course the trail will disappear after some time if the reinforcement is too slow, which may occur when the food source becomes exhausted. The interesting thing is that this trail recruitment system is not only a mechanism used to quickly assemble a large number of foragers around a food source, it also enables a colony to make efficient decisions such as the selection of the shortest path leading to a food source.

In the beginning of the 1990s, Jean-Louis Deneubourg and his collaborators have designed a simple and elegant experiment showing that information can be amplified and selected by ant colonies using pheromone trails (Deneubourg and Goss 1989). In the experiment, an ant nest was connected to a food source with a binary bridge whose branches were of equal length. After a certain period of time, they observed that most traffic occurs on a single branch. The choice was random with approximately 50% of the experiments in which one branch was selected and 50% in which the other branch was selected. Initially, the ant's choice is made at random because there is no pheromone on the branches. As time goes by, the stochasticity of individual decisions causes a few more ants to choose one branch. The greater number of ants on this branch induces a greater amount of pheromone, which in turn, stimulates more ants to choose the branch. This is a positive feedback which amplifies an initial random fluctuation. In the end, most traffic will take place on a single branch, chosen randomly (see Fig. 1(b)).

Today, we know that most collective decisions in social insects arise through the competition among different types of information that can be amplified in various ways. In the case of path selection by ants, the information is conveyed by the pheromone trail. However, environmental constraints, such as the distance between the nest and the food source, affect this positive feedback. In particular, any constraint that modulates the rate of recruitment or the trail concentration on a branch can lead that branch to lose, or win, its competition against the other one (Detrain et al. 2001; Jeanson et al. 2003). Thus, an efficient decision can be made without any modulation of individual behavior and without any sophisticated cognitive processing at the individual level.

This occurs, for example, when a colony of ants is presented with a short path and a long path leading to a food source (Goss et al. 1989). Using the trail-laying trail-following behavior, the shortest branch is selected in most cases. The first ants use both paths to reach the food source. When they come back to the nest, the ones that take the shortest path reach the nest first. The shorter path is thus slightly more marked with pheromone, and is therefore, more attractive to the ants that leave the nest to go to the food source. In this case, the positive feedback amplifies an initial difference induced by the path geometry. This simple experiment shows that geometrical constraints can play a key role in the collective decision-making processes that emerge at the collective level. The colony "as a whole" is able to produce an efficient collective response that far exceeds the scale and abilities of a single individual ant.

2.3 Principles and properties of self-organizing processes

These collective decisions in ants rely on self-organization that appears to be a major component of a wide range of collective behaviors in social insects, from the thermoregulation of bee swarms to the construction of nests in ants and termites (Bonabeau et al. 1997; Camazine et al. 2001). Self-organization is a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among its lower-level components, without being explicitly coded at the individual level. It relies on four basic ingredients:

1. The first component is a positive feedback that results from the execution of simple behavioral "rules of thumb" that promote the creation of structures. For instance, trail recruitment to a food source is a kind of positive feedback which creates the conditions for the emergence of a trail network at the global level.
2. Then we have a negative feedback that counterbalances positive feedback and that leads to the stabilization of the collective pattern. In the example of ant foraging, negative feedback may have several origins. It may result from the limited number of available foragers, the food source exhaustion, and the evaporation of pheromone or a competition between paths to attract foragers.
3. Self-organization also relies on the amplification of fluctuations by positive feedbacks. Social insects are well known to perform actions that can be described as stochastic. Such random fluctuations are the seeds from which structures nucleate and grow. Moreover, randomness is often crucial, because it enables the colony to discover new solutions. For instance, lost foragers can find new, unexploited food sources, and then recruit nest mates to these food sources.
4. Finally, self-organization requires multiple direct or stigmergic interactions among individuals to produce apparently deterministic outcomes and the appearance of large and enduring structures.

In addition to the previously detailed ingredients, self-organization is also characterized by a few key properties:

1. Self-organized systems are dynamic. As stated before, the production of structures as well as their persistence requires permanent interactions between the members of the colony and with their environment. These interactions promote the positive feedbacks that create the collective structures and act for their subsistence against negative feedbacks that tend to eliminate them.
2. Self-organized systems exhibit emergent properties. They display properties that are more complex than the simple contribution of each agent. These properties arise from the nonlinear combination of the interactions between the members of the colony.
3. Together with the emergent properties, non linear interactions lead self-organized systems to bifurcations. A bifurcation is the appearance of new stable solutions when some of the system's parameters change (see Appendix 1). This corresponds to a qualitative change in the collective behavior.
4. Last, self-organized systems can be multi-stable. Multi-stability means that, for a given set of parameters, the system can reach different stable states depending on the initial conditions and on the random fluctuations.

3 Categorizing the collective behaviors of social insects

From the previously described self-organizing processes may emerge a wide variety of collective behaviors that are intended to solve a given problem. Such diversity may give the impression that no common point exists at the collective level between for instance the construction of the relatively simple nest of the ant *Leptothorax albipennis* made up with a single wall of debris and the construction of the seemingly more complex nest of the termite *Macrotermes bellicosus* with its intricate network of galleries and chambers. Nevertheless, it is possible to break down all these collective behaviors into a limited number of behavioral components.

For example, Anderson and Franks (2001) have proposed to separate the collective behaviors accomplished by an insect colony into four task types: individual, group, team and partitioned tasks. Following that categorization of social insects' behaviors, Anderson et al. (2001) have proposed that every global task in a colony (for instance nest construction) can be broken down in a hierarchical structure of subtasks of the previous types. Their method can be seen as the deconstruction of a problem into the basic tasks required to solve it.

Another way to deconstruct the collective behaviors of social insects goes through the functions that organize the insects' tasks. We identified four functions of that kind: coordination, cooperation, deliberation and collaboration (see Fig. 1). They are not mutually exclusive but rather contribute together to the accomplishment of the various collective tasks of the colony. In the following sections, we first provide a definition of each and then illustrate their respective role in some examples of social insects' collective behaviors.

3.1 Coordination

Coordination is the appropriate organization in space and time of the tasks required to solve a specific problem. This function leads to specific spatio-temporal distributions of individuals, of their activities and/or of the results of their activities in order to reach a given goal.

For instance, coordination occurs in the organization of the displacement in bee and locust swarms (Buhl et al. 2006; Janson et al. 2005). In this case, the interactions between individuals generate synchronized (temporal organization) and oriented (spatial organization) movements of the individuals toward a specific goal.

Coordination is also involved in the exploitation of food sources by pheromone trail laying ants. They build trail networks that spatially organize their foraging behavior between their nest and one or more food sources (Hölldobler and Wilson 1990; Traniello and Robson 1995; Wilson 1962).

As a last example, coordination is at work in most of the building activities in insect colonies. During nest building in certain species of social wasps (Downing and Jeanne, 1988, 1990; Karsai and Theraulaz 1995; Wenzel 1996) or termites (Bruinsma 1979; Grassé 1959), the stigmergic process described in Sect. 2.1 favors the extension by an individual of structures (spatial organization) previously (temporal organization) achieved by other individuals.

3.2 Cooperation

Cooperation occurs when individuals achieve together a task that could not be done by a single one. The individuals must combine their efforts in order to successfully solve a problem that goes beyond their individual abilities.

Cooperation is obvious in large prey retrieval, when a single individual is too weak to move a food item. Many cases of cooperative transport of prey were reported for several ant species such as weaver ants *Oecophylla longinoda* (Wojtusiak et al. 1994), army ants *Eciton burchelli* (Franks 1986) or *Formica* wood ants (Chauvin 1968; Sudd 1965). Such cooperative transport of prey can be a very efficient way to bring back food to the nest. For example, in the ant *Pheidologeton diversus*, it was reported that ants engaged in the cooperative transport of a prey can hold at least ten times more weight than did solitary transporters (Moffett 1988).

Cooperation can also be involved in other tasks than prey retrieval. For instance, it is at work in chain formation in the weaver ant *Oecophylla longinoda*. In this ant species individuals hang to each other to form chains allowing the bridging of empty space between two branches or the binding of leaves during nest construction (Deneubourg et al. 2002; Hölldobler and Wilson 1990; Lioni et al. 2001).

A last example of cooperation occurs when a long wood stick is plug into the entrance of an ant nest (Chauvin 1971). In such situation, ants combine their efforts to pull out the stick from the hole. Some of the ants lift the stick up while others slip their head inside the hole, in order to prevent the stick to fall back. Eventually, the combined efforts lead the group to remove the stick from the nest entrance.

3.3 Deliberation

Deliberation refers to mechanisms that occur when a colony faces several opportunities. These mechanisms result in a collective choice for at least one of the opportunities.

For instance, honeybees (*Apis Mellifera*) select the more productive floral parcels thanks to the recruitment of unemployed workers by the waggle dance performed by foragers returning from a food source (Seeley et al. 1991).

When ants of the species *Lasius niger* have discovered several food sources with different qualities or richness, or several paths that lead to a food source, they generally select only one of the different opportunities. In this case, the deliberation is driven by the competition between the chemical trails leading to each opportunity (see Sect. 2.2). In most cases, ants will forage at the richer food source and travel along the shorter path toward the food source (Beckers et al. 1990, 1992; Goss et al. 1989).

3.4 Collaboration

Collaboration means that different activities are performed simultaneously by groups of specialized individuals, for instance foraging for prey or tending brood inside the nest (Gordon, 1989, 1996; Wilson 1971). This specialization can rely on a pure behavioral differentiation as well as on a morphological one and be influenced by the age of the individuals.

The most conspicuous expression of such division of labor is the existence of castes. For instance, in leaf cutter ants workers may belong to four different castes and their size is closely linked to the tasks they are performing (Hölldobler and Wilson 1990). Only the workers whose head size is larger than 1.6 millimeters are able to cut the leaves that are used to grow a mushroom that is the main food source of these colonies. On the contrary, only the tiny workers whose head size is about 0.5 millimeters are able to take charge of the cultivation of the mushroom.

Differently, all workers in Indian paper wasps *Ropalidia marginata* and *Ropalidia cyathiformis*, look alike. But they do not work to the same extent and they do not perform the same kind of tasks. Some of the workers are foragers and take most of the burden of going out of the colony in search of food and building materials. Others specialize in staying and working at the nest. Among these, some are more aggressive towards their nest mates and they are called fighters. The other wasps staying at home are called sitters and spend most of the time just sitting and grooming themselves (Gadagkar and Joshi 1983, 1984).

3.5 Organizing collective behaviors

Most of the collective behaviors in social insects can be understood as a combination of at least two of the four functions of organization defined in the previous sections. To better illustrate this point, we quickly describe in this section two examples of insects' collective behaviors and we break them down as coordination, cooperation, deliberation and collaboration functions.

3.5.1 House hunting in the honeybee

When a bee colony outgrows its hive, the mother queen and nearly half of the workers usually leave their nest. They temporarily form a cluster (called a bivouac) on a tree branch from which they start a complex procedure for finding a new nest site (reviewed by Seeley and Visscher 2004). First, scout bees (about 5% of the bees at the bivouac) explore the environment and search for suitable places to build a new hive. Once a scout bee finds such a place, it comes back to the bivouac where it recruits some other scout bees by performing a waggle dance. In turn, these recruited scouts assess the potential nest site and may possibly perform the waggle dance to recruit other scouts. Thus, a competition arises between different groups of scout bees recruiting for different potential nest sites. Once a site is visited by a sufficient number of scout bees, these latter advertise the rest of the cluster that it is time to warm up their flight muscles and to prepare for the liftoff toward the new nest site. They use three distinct signals to that purpose: the shaking signal that activates the quiescent bees, the piping signal that initiates the warm-up of the flight muscles and the buzz running signal that prepares bees for the liftoff (Seeley and Tautz 2001).

At least three organization functions participate to the migration of honeybees toward a new nest site. First, collaboration occurs since bees split in two different functional groups: scout bees that search for potential nest site and clustered bees that remain quiescent and conserve the colony's energy reserves. Second, a self-organized deliberation process leads to the choice of a suitable place for nesting among several opportunities. And third, the quasi simultaneous liftoff of all bees in the cluster obviously results from a coordination function mediated by the three liftoff preparation signals.

3.5.2 Nest construction in the weaver ant

Nest in the weaver ant *Oecophylla longinoda* are made of leaves stuck together (Hölldobler and Wilson 1990; Ledoux 1950). The nest construction requires the repetition of two stages: assembling two leaves and gluing them. In the first stage, workers line up in a row along the margin of a leaf and pull together to bring closer the two leaves (see Fig. 1(c)). If the gap between the two leaves is longer than a single ant, workers form a chain with their own bodies. Then, they pull together as one individual to bring them closer. In the second stage, when the leaves have been put in place, other workers carry mature larvae and use the silk they produce to glue the leaves together (see Fig. 1(d)).

Nest construction in the weaver ant requires several functions of organization to be successfully achieved. It first needs a coordination function to ensure that leaves are put together before being glued. It also needs two cooperation functions. The first one occurs when workers pull together the leaves since this task can not be performed by a single one. The second arises during the gluing of the leaves: workers that do not produce silk require larvae that can not move alone. At last, a collaboration function distributes the tasks between different groups of individuals: workers that pull and maintain the leaves appropriately, workers that carry the larvae and larvae that produce the silk for gluing the leaves.

3.5.3 Conclusion

As exemplified in the two previous subsections, the organization of collective behaviors in social insects can be understood as the combination of the four coordination, cooperation, deliberation and collaboration functions. Each of these functions emerges at the collective level from the unceasing interactions between the insects. They support the information processing abilities of the colony according to two main axes:

(1) Coordination and collaboration shape the spatial, temporal and social structures that result from the colony's work. The coordination function regulates the spatio-temporal density of individuals while the collaboration function regulates the allocation of their activities.
(2) Cooperation and deliberation provide tools for the colony to face the environmental challenges. The deliberation function represents the mechanisms that support the decisions of the colony, while the cooperation function represents the mechanisms that overstep the limitations of the individuals.

Together, the four functions of organization produce solutions to the colony problems and may give the impression that the colony as a whole plans its work to achieve its objectives.

4 Modulation of self-organized behaviors

In the preceding sections, we have seen that the organization of the collective behaviors in social insects arises from four functions that emerge from the activities of a dense network of interactions. These interactions take place among the members of a colony and between them and their environment. Because the colony and its environment permanently evolve in time, they can be considered as coupled dynamic systems.

However, inside a colony of insects, some features seem to be actively maintained constant and thus get out from the dynamic evolution of the colony. For instance, a humidity drop can be life-threatening for cockroaches that could die as a consequence of desiccation. To avoid the death, cockroaches maintain locally a sustainable humidity level thanks to an increase of their tendency to aggregate (Dambach and Goehlen 1999). As another example, when their colony size varies, ants of the species *Leptothorax albipennis* are able to maintain their nest size so that each adult worker has about 5 mm^2 of floor area in the nest (Franks et al. 1992). In these two cases, the colony modifies its behavior in order to counterbalance the effects of a potentially harmful perturbation. The insect colony is thus an adaptive system. Now the question is: what are the mechanisms that underlie collective adaptation in insects' societies?

The only way for a colony to adapt its collective behavior is through the modulation of individual insect behaviors. With the term "modulation" we suggest that the probability for a given behavior to occur varies according to the disturbance. Each individual is able to sense the variation thanks to local cues and it slightly modifies its behavior in response. These behavioral modifications affect the interaction network, and hence the global structure, through a new balancing of positive and negative feedbacks.

4.1 Factors that modulate self-organized behaviors

Two kinds of perturbations modulate self-organized biological behaviors. The first ones are produced by changes in the environment. We call them "outer colony" factors because they arise independently of the insect colony. These factors comprise climatic parameters such as temperature, humidity or wind, and ecological parameters such as food distribution or predator presence.

We call "inner colony" factors the second kind of perturbations affecting self-organized biological behaviors. These factors are directly linked to the colony or its components: the size (i.e., the total number of individuals that belong to the colony), the morphological differences between insects (i.e., the ratio of the different physical castes), learning, etc.

Inner and outer factors both influence insect behavior. And the result of the insects' activities can, in return, influence outer and inner factors. For example, air flows modulate the corpse clustering behavior of the ant *Messor sanctus* and are, in return, deviated by the insects' construction (Jost et al. 2007). The successful achievement of a task can improve the experience of an individual which, in return, may favor the future achievement of the same task (Theraulaz et al. 1991). Thus, a subtle network of interacting influences regulates individual behaviors and provides to the colony a real-time solution to a real-time problem.

4.2 Three examples of modulation

Whatever the nature of the perturbation, one must answer the two following questions to identify the mechanisms that underlie a collective adaptation to a given perturbation in an insect colony.

(1) How does the perturbation modulate the individual behaviors of the interacting animals? Does it stimulate animals to perform a particular behavior or task or does it prevent them from doing so?
(2) How does the modulation of the individual behavior shape the properties at the collective level? What changes does it trigger in the interaction network? What new structures does it elicit when the group behavior is considered?

In order to better illustrate the previous questions, we present in the rest of this section, three examples of self-organized biological behaviors and their modulation by inner and/or outer factors. In each case we describe the mechanism in terms of individual behaviors, its result at the collective level and the impact of the modulation of individual behaviors by one or several factors.

4.2.1 Corpse clustering in ants

Numerous ant species carry their dead out of the nest and aggregate them near the nest entrance (Ataya and Lenoir 1984; Haskins and Haskins 1974; Howard and Tschinkel 1976). This behavior has been studied in the lab under controlled conditions with *Messor sanctus* ants. When corpses are spread over the whole surface of an arena, ants collect and aggregate the corpses within a few hours. In the beginning, several clusters are formed and compete with each other to attract ants carrying corpses, and in the end only the piles that succeed to grow faster than the others will persist (Theraulaz et al. 2002).

To build these structures, ants pick-up and drop a corpse as a function of the density of corpses they detect in their local neighborhood. We can have an estimate of these probabilities by looking at the behavior of ants when they come into contact with corpse piles of increasing size. The greater the size of a pile, the less likely the ant will pick up a corpse on that pile. On the other hand, the dropping probability increases rapidly as a function of the size of the pile. Thus, a positive feedback results from the combination of both enhancement of the dropping behavior and inhibition of the picking up behavior. This process is similar to the one that led to the formation of foraging trails, with the difference that here the negative feedback results from the depletion of isolated corpses that prevents the formation of other clusters in the neighborhood of a cluster already in place.

In laboratory conditions with stable environmental factors, this corpse picking-up and dropping behavior results in few persisting piles with a circular shape. Interestingly, in the presence of a continuous laminar low speed air flow the form of the piles drastically changes. From an almost circular shape they switch to an elliptic one: piles are elongated to create

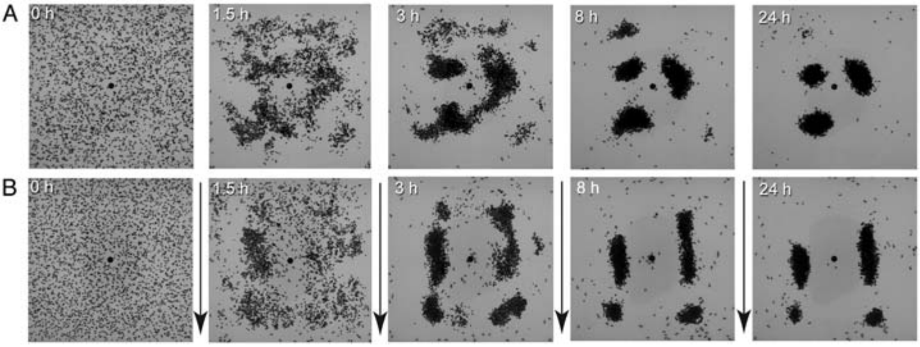

Fig. 3 Spatio-temporal dynamics of corpse clustering by ants *Messor sanctus* without (**a**) and with (**b**) air currents. Black dots are ant corpses and black arrows indicate the air flow direction (from Jost et al. 2007 with permission)

parallel "walls" in the same direction as the wind (see Fig. 3). Note that the air flow is too weak (around $1\ \mathrm{cm\,s^{-1}}$) to move a single corpse and thus cannot explain pile elongation by its own. Something must have changed in the behavior of corpse carrying ants.

A recent work has investigated these individual behavioral changes and has linked them to the observed shape modification in the presence of an air flow (Jost et al. 2007). Jost and his collaborators have shown that the probability to pick up a corpse from a pile grows with air flow speed while the probability to drop a corpse decreases with it. They, therefore, conclude that the lower the wind speed, the higher the amplification of corpse clustering. This leads ants to clear corpses from areas of high wind speed and to aggregate them in areas of low wind speed. In addition, they showed with numerical simulations that corpse piles modify the air flow around them: they slow it down on the side facing the wind (front side) and on the lee side; they accelerate it on the other sides. Together with the previous result, this explains why corpse piles lengthen in the same direction as the wind: amplification of clustering is stronger at the front and lee side of the piles. Consequently, a pile will grow from these two sides and will be elongated in the same direction as the wind.

This example illustrates the modulation of a self-organized behavior by an outer colony factor through the modification of individual behavior. Ants aggregate corpses in piles that locally modify air flow. This modification triggers a modulation of individual probabilities to pick-up and drop corpses around the piles. The result is the appearance of a new spatial structure.

4.2.2 Division of labor in wasps

Self-organized processes are also a major component of the division of labor in a colony. For instance in Polistes wasps, division of labor is based on behavioral castes, and the task allocation process results from a complex set of interactions among insects and the brood state (Theraulaz et al., 1991, 1992). In the Polistinae, sudden changes occur in the organization of work when colony size increases (Karsai and Wenzel 1998).

We have experimental evidence showing that each insect has different response thresholds for each of the different tasks to be done (see for instance Deneubourg et al. 1991 for ants; Robinson 1992 and Pankiw et al. 2001 for bees; Weidenmüller 2004 for bumblebees). These response thresholds control the probability for a wasp to perform a task. It depends both on the threshold value and the stimulus level associated with the task at a given time.

Moreover, these response thresholds change with the wasp's experience (Theraulaz et al. 1991). The more an individual works on a task, the lower becomes the threshold for that task. As a consequence, the wasp will be more responsive to small variations of the stimuli. This is another example of a positive feedback loop. Conversely, if the wasp is not performing the task, because she is working on a different task or doing nothing, the threshold will increase. This means that the wasp will be less responsive to the stimuli and the probability to perform the task will be lower. This induces a negative feedback. Similar processes have been described in bumblebees in the context of nest thermoregulation (Weidenmüller 2004). So, when several insects are in competition to perform a task, the combination of the response threshold reinforcement and the competition among insects to perform the task induces the differentiation of individuals and thus the division of labor at the colony level (Theraulaz et al. 1998b). This mechanism creates not only a differentiation among individuals, but it also ensures the adjustment of the ratio of workers engaged in the various tasks and then plasticity of the division of labor.

Now, why do we observe an increase of differentiation among individual activity levels when colony size is increasing? In other words, how does colony size (inner colony factor) modulate the individual behavior of wasps so that the allocation of building tasks strongly differs between small and large colony?

Theoretical results have shown that when the total amount of workload is proportional to the size of the colony (that is, when the mean workload per individual remains constant), there exist large fluctuations of the task associated stimuli in a small colony (see Fig. 4, Appendix 1). As a consequence the positive feedback loops are impeded by the high level of noise and individuals do not differentiate. On the contrary, the greater is the colony size, and thus the higher is the absolute value of the number of tasks to be done, the smaller become the fluctuations of the stimuli, and therefore, the greater are the chances that some of the individuals develop in hard workers (Gautrais et al. 2002). The whole process does not only induce a differentiation in the activity levels among insects, it also induces the specialization of the hard workers in specific tasks. For instance in wasps, the normal sequence of tasks involved in nest building first starts with collecting water, then the wasp searches for wood pulp and finally she comes back to the nest where she molds the pellet and builds a cell. What has been noticed is a general tendency for each wasp to be specialized in the execution of one of these three tasks as the colony size is increasing (Karsai and Wenzel 1998). This means that wasps specialized in water or pulp retrieval must exchange their collected material with cell-building wasps when they come back to the nest. Thus, besides the specialization of workers, the colony size increase also promotes a higher degree of coordination between individuals.

In wasp colonies, division of labor and task specialization result from a combination of a reinforcement process and a competition among individuals to perform the tasks. With these processes the organization of division of labor is automatically adapted when colony size is changing. When the total workload is high, which is the case in a large colony, it is better to have specialized workers whose performance in task execution will be optimal instead of having generalist workers with a lower performance. On the contrary, when the total amount of work is small, which is the case in a small colony, it might be more relevant to have generalist workers. Indeed, it would be too costly to keep specialized workers because these specialists would not work frequently and so they would not be used in an optimal way. So with this self-organized process, a colony is able to collectively optimize the division of labor, with a minimal complexity of the behaviors and cognitive processes which are required to achieve this regulation.

4.2.3 Nest choice in ants

When the nest is destroyed or does not fulfill its requirements anymore (size, humidity, temperature, etc.), ant colonies hunt for new opportunities to settle in their environment. Scout ants seek for suitable places and then recruit their nest mates toward these locations. If several suitable places exist, the colony has to make a choice between the alternatives. This collective decision is done through the recruitment process. Two different recruitment mechanisms toward a new nest location are well studied in ants: mass recruitment and quorum sensing.

Ants of the species *Messor barbarus* use a mass recruitment mechanism to select a new nest site (Jeanson et al. 2004). This mechanism is similar to the one described in Sect. 2.2 in the context of foraging: nest location is selected thanks to a differential amplification of the pheromone trails leading to the different places. The final choice of the colony can be modulated by the quality of the potential nest sites. For instance, dark places are strongly favored against light ones. Interestingly, this choice does not rely on a direct comparison of the different opportunities by ants: facing two different potential nest locations, only 5% of the scout ants that discover one of the two alternatives visit the other one (Jeanson et al. 2004). In fact, the modulation of this collective choice relies on the modulation of the individual trail laying behavior of ants: dark places increase intensity and frequency of trail laying. This modulation of the individual behavior of ants paired with the amplification process of the pheromone trail bias the final collective decision toward the choice of a dark place. However, this situation differs from the differential choice of the shortest path toward a food source seen in Sect. 2.2. In the case of nest choice, no environmental constraint acts on the collective decision of the colony, this latter being only influenced by a natural preference for dark places expressed by ants in the form of a variation of trail laying behavior.

Ants of the species *Leptothorax albipennis* use a completely different recruitment process for choosing a new nest location. This recruitment process called “quorum sensing” takes place in two successive steps (Pratt et al. 2002). First, scout ants that discover a suitable place come back to the old nest and recruit a nest mate by leading a tandem run: the recruiter slowly leads a single recruit from the old nest to the potential new nest. Here the recruited ant assesses by itself the qualities of the potential nest place before recruiting a further nest mate by leading its own tandem run. The quality of the nest modulates the duration of the assessment period: a better nest is assessed more rapidly. It then induces a traffic flow which grows more rapidly. Thanks to this modulation, the numbers of ants in the different potential nest sites slowly diverge. Second, when the number of nestmates in one of the potential nest sites rises above a “quorum” (i.e., the minimal number of individuals that must be present in order for a decision to be taken) the recruitment behavior of ants in this place switches from tandem runs to direct transport by simply carrying the passive nestmates from the former nest. This recruitment by transport is three times faster than recruitment by tandem runs (Pratt et al. 2002). The amplification of the initial choice is so important that the old nest is moved to the new site before other potential sites reach the quorum. Therefore, the collective choice of a nest site in *Leptothorax albipennis* is based on a threshold-based amplification (also called quorum sensing) by the modulation of the individual recruitment behavior.

In the two examples of nest choice described above, modulation of individual behavior by outer or inner colony factors deeply modifies the outcome at the collective level. In the case of ants *Messor barbarus* the modulation of the trail laying behavior by environmental conditions ensures that the colony “as a whole” compares the different opportunities and chooses the best nest site whereas a very small number of ants actually visited all the alternatives. Without such a modulation, the colony would remain able to choose a nest site but only at random.

In quorum sensing by ants *Leptothorax albipennis*, the modulation of recruitment behavior by the number of nestmates in the new nest is an essential part of the mechanism of the decision: it provides the amplification process required to make the decision once the potential nest site was evaluated and approved of by a sufficiently large number of nestmates. Interestingly, this amplification mechanism can be also modulated to adapt the decision making process of the colony to different environmental conditions. By decreasing the quorum value, these ants are able to quicken the choice of a nest if the pressure for emigrating is high (Franks et al. 2003). Conversely, if no particular pressure for emigrating exists, these ants increase the quorum value and thus make more accurate the comparison between the nests (Dornhaus et al. 2004).

5 Managing uncertainty and complexity with swarm intelligent systems

We have seen that complex colony-level structures and many aspects of the so-called swarm intelligence of social insects can be understood in terms of interaction networks and feedback loops among individuals. These are the basic elements that allow the emergence of dynamic patterns at the colony level. These patterns can be material (e.g., corpse clustering, nest building) or social (e.g., division of labor) and lead the colony to structure its environment (e.g., during nest building) and solve problems (e.g., collective decision).

The most interesting properties of these self-organized patterns are robustness (the ability for a system to perform without failure under a wide range of conditions) and flexibility (the ability for a system to readily adapt to new, different, or changing requirements). Robustness results from the multiplicity of interactions between individuals that belong to the colony. This ensures that, if one of the interactions fails or if one of the insects misses its task, their failure is quickly compensated by the other insects. This also promotes stability of produced patterns whereas individual behaviors are mostly probabilistic.

Flexibility of self-organized systems is well illustrated by the ability of social insects to adapt their collective behaviors to changing environments and to various colony sizes (Deneubourg et al. 1986). These adaptations can occur without any change of the behavioral rules at the individual level. For instance, in the case of the selection of the shortest path in ants, a geometrical constraint applied on one of the two alternative paths increases the time needed by the ants to come back to their nest through this path and thus biases the choice toward the other path without any modification of the insects' behaviors.

But flexibility can also rely on the modulation of the individual behavioral rules by some factors produced by the environment or by the activity of the colony. For instance, the presence of an air flow modifies the probability for an ant to pick up and drop corpses of dead ants. This subtle modification of behavioral probabilities deeply modifies the shape of the piles resulting from the ants' aggregating activity (see Sect. 4.2.1). As another example, the modulation of the trail laying behavior as a function of the food source profitability in the ants *Lasius niger* (Beckers et al. 1993) and *Monomorium pharaonis* (Sumpter and Beekman 2003) leads the colony to efficiently select the most rewarding food source if several opportunities are discovered simultaneously. The nutrient demand of the colony can modify the behavior of scout ants and can result in an adjustment of the harvesting strategy in the ant *Lasius niger* (Portha et al., 2002, 2004). The ability of a single worker to retrieve a prey modifies its recruiting behavior and generates a diversity of collective foraging pattern in the ant *Pheidole pallidula* (Detrain and Deneubourg 1997). Last, the presence of environmental heterogeneities can modulate the behavior of an insect and thus bias the behavior of the colony toward a particular solution (Dussutour et al. 2005).

All these behavioral modulations provide the opportunity for a colony to develop a wide range of collective behaviors and can also be a powerful lever for evolution to shape and optimize these behaviors in a highly adaptive way. Thanks to the sensitivity of individuals to variations (either environmental or triggered by the colony itself), the colony as a whole is able to perceive these changes and can thus react appropriately in almost every situation.

For the sake of simplicity, previous models of self-organized behaviors in insect societies often assumed that animals follow some kind of fixed behavioral rules and that new collective structures appear after the system has reached a bifurcation point. If such a viewpoint is of great interest to understand the mechanisms underlying a given collective behavior, one must keep in mind that the natural context in which it occurs can vary from day to day (or even from hour to hour) and that insect colonies have to permanently adapt their behavior to changing conditions. For this reason, future studies in social insects should emphasize the role of individual behavioral modulations in the flexibility of self-organized behaviors. Indeed these modulations trigger new interesting questions about the way insect societies deal with unpredictable and complex environments. For instance, it would be interesting to know how many "modulated" individuals are required to significantly influence the collective output (Couzin et al. 2005; Gautrais et al. 2004) or how much time is needed for the system to adapt its global behavior to the perturbations. These quantities can be viewed as the sensitivity and reactivity of the system to the perturbations.

It would also be interesting to question at which conditions individual behavioral modulations are efficient to produce flexible responses at the level of the colony (see Appendix 2). Switching from a collective structure to another one which is better suited to the current situation requires at least that this switch is indeed possible. The following example illustrates the problem. The black garden ant *Lasius niger* and the honey bee *Apis mellifera* both recruit their nest mates toward newly discovered food sources. Scout ants use a pheromone trail to lead uninformed workers to the food source while scout bees indicate its location thanks to their well-known waggle dance. If one provides a bee or an ant colony with two different food sources, a poor one and a rich one, at the same time, then ants and bees will be able to select the richest one. But if one provides the poor source first, lets the colonies establish a recruitment toward this source and then introduces the rich source, then only the bees will be able to switch their recruitment toward this new source (Camazine and Sneyd 1991). Ants will continue to preferentially forage on the less rewarding food source (Beckers et al. 1990). The parameters of their recruitment mechanism do not allow them to change their collective behavior to a more profitable one, as bees do.

This problem of ants being stuck in a less favorable collective behavior was addressed in (Bonabeau 1996). Bonabeau showed with the help of a simple model of cooperative foraging that the parameters of the recruitment behavior can lead to an efficient and flexible behavior only if the corresponding stable state is on the one hand close to a bifurcation point and on the other hand in a region where structures can appear and last. If the system at its stable state is too far from a bifurcation point, it becomes hard to make it behave differently and it may remain stuck in a sub-profitable solution. Thereby it should be relevant for a colony to have a mechanism that keeps the collective output at the edge of a bifurcation, not too close so that structures appear and are maintained, but also not too far so that they remain readily adaptive (see Appendix 2). This could be the purpose of the modulations of individual behaviors.

6 Conclusions

Understanding how self-organization works in social insects has already inspired numerous algorithms to control the collective behavior of artificial systems (Bonabeau et al. 1999). However, the recent discoveries about the role individual behavioral modulations play in the adaptive abilities of insect colonies suggest us that the biological study of swarm intelligent systems should provide new sources of inspiration for the design of control algorithms. In particular, giving to artificial agents the ability to modulate their individual behaviors according to cues partially reflecting at the individual level the modifications that occur at the level of the colony would make this artificial colony better prepared to deal with uncertain worlds. Such agents would be able to collectively anticipate negative side effects due to the evolution of their own colony or to counterbalance the impact of hazardous environmental changes.

The transition from "self-organization" to "self-organization plus self-adaptation" should trigger an increase of complexity in the tasks or the environments an artificial colony could deal with. The addition of self-adaptation to self-organization multiplies the number of group patterns and collective behaviors that can be potentially displayed by the artificial colony. Interestingly, this does not necessarily mean that the behavioral complexity required at the agent level is also dramatically increased. Actually, the major modification of the individual behavioral controller should be a transition from fixed probabilities to accomplish tasks to varying ones. This variation would be an appropriate function of a local cue that correlates with the perturbation the global system would face.

In conclusion, the increased flexibility of collective structures in an insect colony triggered by simple modulations of the individual behavior opens interesting ways toward the design of self-adaptive artificial swarm intelligent systems. The pursuance of experimental investigations in biological systems and the development of new theoretical frameworks about the adaptive role of these modulations should encourage the emergence of new applied studies. This lets us believe that the potential of swarm intelligence is far from being exhausted.

Appendix 1 Bifurcations in self-organized behaviors

The dynamics of self-organized biological systems are shaped by the amplification of random fluctuations through positive feedback loops. Such dynamical systems can display bifurcations in the space of solutions, depending on a driving parameter. Above a critical value, the system can reach new stable states whereas the old solution becomes unstable.

In social insects, the dynamics of collective behaviors are intrinsically stochastic and discrete but in some cases they can be approximated by a system of non-linear differential equations, such as in the collective choice of a foraging path in ants.

Let us consider ants leaving their nest and facing a choice between two bridges leading to the same food source. In the absence of clues, each ant will choose either of these bridges with equal probability. If, however, preceding ants have left some pheromone on the bridge they took, then the incoming ants prefer to walk on the bridge over which the pheromone concentration is higher. This is a positive feedback loop: the more a bridge is chosen, the more likely it will be chosen by ants.

For the very first ants facing the choice, the concentrations of pheromone on both bridges are very low and their difference is difficult to assess. Hence, their choices are still more or less equal between the two bridges. When the fluxes of ants reach a critical value, this difference becomes significant and triggers the positive feedback loop. Here, the flux of incoming ants acts as a driving parameter.

Let C_1 and C_2 be the concentrations in pheromone on bridges 1 and 2. An ant leaving the nest will face the two bridges and choose the bridge C_i with probability:

$$p(C_i|C_1,C_2)=\frac{(k+C_i)^\alpha}{(k+C_1)^\alpha+(k+C_2)^\alpha},\quad i=1,2$$

where k and α are parameters specific to the ant species and the actual set-up. If we assume the simplification that an ant deposits one unit of pheromone each time it takes a bridge, C_i represents the flux of ants on the bridge i. The dynamics can thus be approximated by:

$$\frac{dC_i}{dt}=\Phi p(C_i|C_1,C_2)-\mu C_i,\quad i=1,2$$

where Φ is the total flux of ants leaving the nest, and μ the characteristic time of pheromone evaporation.

This equation can be adimensionalized using:

$$\begin{aligned}&C_i\to kc_i,\\&t\to\tau/\mu,\\&\phi\to\Phi/(k\mu)\end{aligned}$$

yielding

$$\frac{dc_i}{dt}=\phi\frac{(1+c_i)^\alpha}{(1+c_1)^\alpha+(1+c_2)^\alpha}-c_i,\quad i=1,2.$$

Hence, at the equilibrium, $\frac{dc_i}{dt}=0$, $i=1,2$, we have:

$$c_i=\phi\frac{(1+c_i)^\alpha}{(1+c_1)^\alpha+(1+c_2)^\alpha},\quad i=1,2.$$

Experimental studies estimated $\alpha=2$ and $k=4$ in *Lasius niger* (Beckers et al. 1990, 1992, 1993). Using these parameters, and $c_1+c_2=\phi$, solutions are such that:

$$(c_i-\phi/2)\big(c_i^2-\phi c_i+1\big)=0,\quad i=1,2$$

which yields three equilibrium states:

$$(c_1,c_2)=\left(\frac{\phi}{2},\frac{\phi}{2}\right),\tag{1}$$

$$(c_1,c_2)=\left(\frac{1}{2}\big(\phi+\sqrt{\phi^2-4}\big),\frac{1}{2}\big(\phi-\sqrt{\phi^2-4}\big)\right),\tag{2}$$

$$(c_1,c_2)=\left(\frac{1}{2}\big(\phi-\sqrt{\phi^2-4}\big),\frac{1}{2}\big(\phi+\sqrt{\phi^2-4}\big)\right).\tag{3}$$

The solution (1) corresponds to an equal use of the two bridges: this is a no-choice solution, whereas solutions (2) and (3) correspond to an asymmetrical use of the bridges: they are a collective choice (Fig. 4A, B).

There is a bifurcation because solutions (2) and (3) only exist for $\phi>2$.

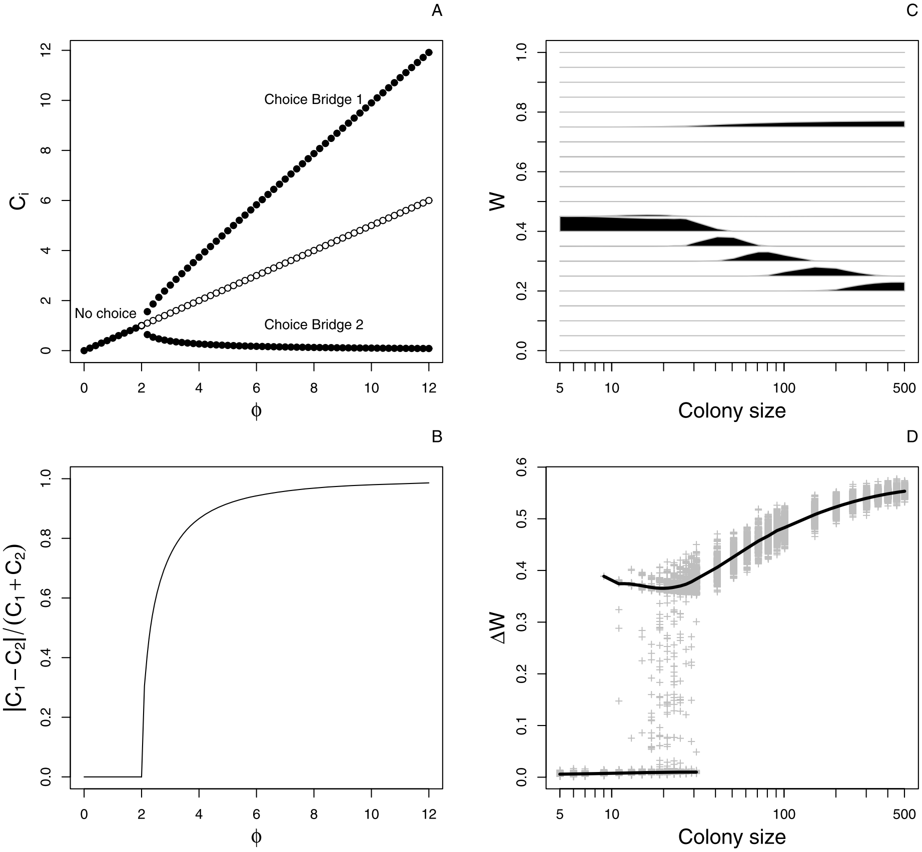

Fig. 4 **A** The stable solutions for the flux C_1 of ants on the bridge 1 (*plain dots*) as a function of the incoming total flux ϕ. The system exhibits a bifurcation at $\phi_c = 2$ beyond which the no-choice solution becomes unstable (*open dots*) and the fluxes become asymmetrical, either at a high level on bridge 1, or at a high level on bridge 2. **B** The differentiation of the flux on the two bridges occurs only above the critical total incoming flux $\phi_c = 2$. The differentiation was computed as the absolute value of the relative difference of the fluxes on each bridge shown in subfigure (**A**) above. **C** The distribution of individual working times W (y-axis) for increasing colony sizes (x-axis). In small colonies, all individuals work at the same rate (about 40% of their time are devoted to the task), whereas for large colonies only a few individuals work at a high rate (75%) while the others do not work much (20%). For each colony size, the distribution is an average over 1000 simulations for 200 000 time steps. **D** The differentiation ΔW of the working times occurs only above a critical colony size ($N = 20$–30). For each simulation used for subfigure (**C**) above, the differentiation ΔW (dots) was computed as the difference of working time between the most working and the less working individuals in the colony. The lines indicate the mean differentiation levels among the undifferentiated colonies ($\Delta W \approx 0$) and the highly differentiated colonies ($\Delta W \geq 0.3$)

Hence $\phi = 2$ is the critical flux which elicits a bifurcation in the space of solutions: if the total flux of ants leaving the nest is too low, the dynamics can not yield the collective choice solutions.

Furthermore, beyond this critical value, the no-choice solution (1) becomes unstable. Hence, the random fluctuations around the equal use of bridges will trigger the positive feedback loop and lead the system to one of the two collective choice solutions. Since ants are actually a discrete system, one can be sure that the fluctuations are always sufficient for destabilizing this no-choice solution.

Note that the adimensionalized variable representing the flux ϕ is such that the corresponding critical flux Φ is proportional to the evaporation rate of the pheromone: the faster the pheromone evaporates, the greater the minimal flux to yield a collective choice.

As a whole, the collective choice emerges provided that the flux of ants is sufficient to compensate the pheromone evaporation.

In this first example, the bifurcation process leads the colony to drive all the individuals to make eventually the same choice. As far as the individual behaviors are concerned, this is a bifurcation which homogenizes the individual choices.

In other cases, the bifurcation can lead by contrast to break the homogeneity of the behaviors, as it is the case in a model of the division of labor in wasps' colonies (Gautrais et al. 2002).

In this model, the colony has to perform work for tackling a task T. Individuals can engage in doing the task, performing α units of work per unit of time. The task has an associated stimulus S that can be perceived by all individuals. If no wasp is currently working, the task spontaneously increases at a constant rate σ. Hence:

$$dS = (\sigma - K(t)\alpha)dt, \qquad S(0) = 0$$

where $K(t)$ is the number of workers devoted to the task at time t. To simplify the comparison between different colony sizes, σ is kept proportional to the colony size N.

For each individual i, the decision to perform the task is stochastic and depends on an internal threshold Θ_i, according to:

$$P(i \text{ engages}) = \frac{S^2}{S^2 + \Theta_i^2}.$$

If the threshold is low, $\Theta_i \ll S$, individual i is very prone to engage in the task. Once engaged in the task, the individual stops working at a constant rate p.

If all individuals have random threshold, the allocation of work among the workers would simply reflect the underlying distribution of thresholds. However, this distribution would have to be "well-shaped" for the system to fulfill the basic requirement of allocating the right number of workers to the task and keep the stimulus at a minimal level. This well-shaped distribution would depend on the balance between the increase of the amount of work to be done (σ), the individual parameters (p and α) and the number of available workers, that is, the size of the colony (N). Designing this distribution on an individual basis would require that insects had access to global information (N, and the threshold of others) which is hardly conceivable.

We proposed a mechanism of adaptive threshold that can produce such a distribution, using only the information provided by the stimulus level.

Thresholds adapt according to the following rule: an individual engaged in the task gets a lower threshold for the task whereas an idle individual gets a higher threshold for the task. This positive feedback is expressed as:

$$d\Theta_i = \big(-\xi I_i + \varphi(1 - I_i)\big)\, dt$$

where $I_i = 1$ if i is engaged in the task, 0 otherwise. (ξ, φ) are, respectively, thresholds reinforcement and forgetting parameters. Thresholds are kept in a limited range from 0 to $\Theta_{\max}$ that acts as a negative feedback which stabilizes the process.

With this simple individual rule, a suitable distribution of thresholds spontaneously emerges in a colony starting with all individuals having the same initial threshold (0).

For some values of (ξ, φ), the system can furthermore exhibit a striking property of the division of labor in social insects, namely that the individuals differentiate their working time only in large colonies (Fig. 4C, D).

This size-induced bifurcation originates in the granularity of the stimulus fluctuations that can trigger or not the positive feedback on the thresholds. In small colonies, the amounts σ of work to be done, and α of work done by one individual are of the same order so that the variation of the number of working individuals induces great variations of the stimulus. As a consequence, even the workers with high thresholds have a significant probability to perform the task when by chance the stimulus becomes low. On the contrary, in large colonies the impact of the work done by one worker becomes negligible so the stimulus weakly fluctuates around a constant value. As a consequence, the individuals with high thresholds have a vanishing probability to perform the task (and their thresholds become even higher), and only those workers that have a low threshold can be enrolled (and their thresholds stabilize at a low value).

Appendix 2 Modulation of individual behaviors and collective response tuning

In the first approximation of the collective choice by ants presented in Appendix 1, the individual choice function takes for granted that individuals can perceive pheromone levels with no restriction:

$$p(c_1) = \frac{(k + qc_1)^2}{(k + qc_1)^2 + (k + qc_2)^2} \tag{4}$$

where q represents the amount of pheromone left by an individual, c_1, c_2 the fluxes on the two bridges, and k a constant related to the perceptual discriminative power for pheromones.

However, we know that in general perceptual devices only respond to a limited range of stimuli, and can saturate when the stimulus becomes too high. In the present case, this can be taken into account by considering that the individuals estimate the flux on bridge $\tilde{c}_1$ through a saturating function of the actual amount of pheromone qc_1. This function can be modeled as:

$$qc_1 \rightarrow \tilde{c}_1 = \frac{2c_s (qc_1)^2}{c_s^2 + (qc_1)^2} \tag{5}$$

where c_s represents the saturating value (Fig. 5A). Plugging (5) into (4) yields:

$$\frac{dC_i}{dt} = \Phi \frac{(k + \frac{2c_s(qc_i)^2}{c_s^2+(qc_i)^2})^2}{(k + \frac{2c_s(qc_1)^2}{c_s^2+(qc_1)^2})^2 + (k + \frac{2c_s(qc_2)^2}{c_s^2+(qc_2)^2})^2} - \mu C_i, \quad i = 1, 2 \tag{6}$$

which can have up to five real stationary solutions depending on the total adimensionalised flux $\phi = \Phi/\mu$.

Interestingly, for low values of ϕ, the system with perceptual saturation behaves similarly as in the first approximation with no saturation, including the bifurcation to the collective choice above a critical lower flux ϕ_m (compare Fig. 5B with Fig. 4A, Appendix 1). However, for higher fluxes the perceptual saturation at the individual level prevents the emergence of a collective choice at the colony level because both bridges appear equally attracting even

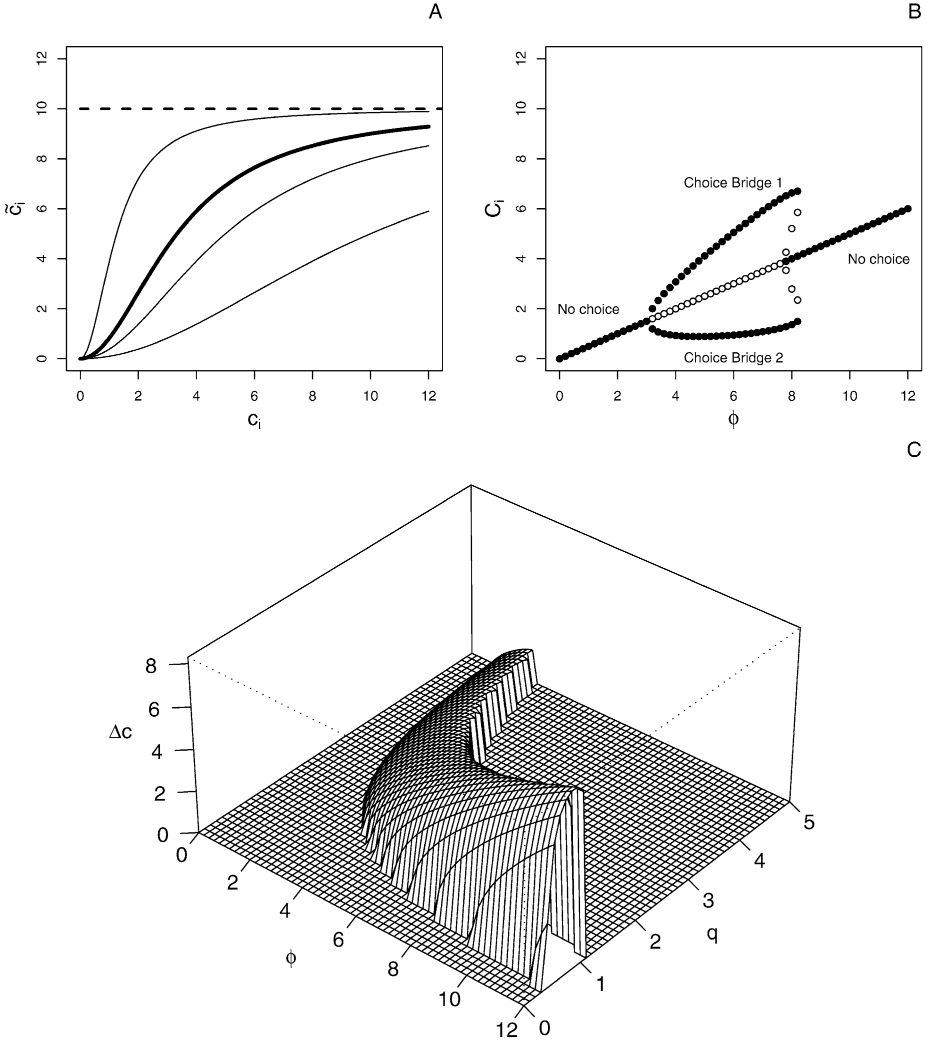

Fig. 5 **A** Estimation $\tilde{c}_1$ of the actual flux c_1 when the perceptual device is saturating at c_s (arbitrarily fixed to 10). Since the saturation pertains to the pheromone, $\tilde{c}_1$ depends on the amount of pheromone q that each individual ant lays down. For higher values of q, the saturation occurs for lower values of the flux (from left to right, $q = 4, 1.5, 1, 0.5$). **B** The stable solutions for the flux C_1 on the bridge 1 (*plain dots*) as a function of the incoming total flux ϕ. The system exhibits the collective choice (asymmetrical fluxes) only for a range of ϕ. The solutions presented correspond to $q = 1.5$, marked as *bold line* in (**A**). **C** The ranges of fluxes that elicit a collective choice as a function of the individual deposit q. The collective response (z-axis) is indicated by the asymmetry of the fluxes on the two bridges $\Delta c = \frac{|c_1 - c_2|}{c_1 + c_2}$. $\Delta c > 0$ indicates the emergence of the collective choice

if the actual fluxes are not similar. Hence, there exists a critical upper flux ϕ_M above which the collective choice vanishes.

From a computational point of view, the collective choice can be considered as a response of the colony to the environmental conditions, either external (as in the case of bridges of different length) or internal such as the number of foragers.

In the simplest case with no perceptual saturation, the system behaves as a high-pass filter (it responds only to high incoming fluxes). Introducing the saturation constraint on individual perceptual ability enables the system to behave like a bandpass filter: it responds then to a specific range $\phi_m \cdots \phi_M$ of the total flux ϕ.

The bandwidth of this collective response depends non-linearly on the amount of pheromone q left by each individual (Fig. 5C). For high values of q, the system exhibits a collective choice for lower values of ϕ, but saturates quickly. Correspondingly, for a given flux ϕ, the collective choice can emerge only for a limited range of q. This range shrinks for higher values of ϕ: an increasing number of individuals at play increases the accuracy of the response. The collective response of the colony can thus be tuned by modulating individual parameters.

From a functional point of view, the collapse of the collective choice for higher flux values might be an unwanted side effect of the perceptual saturation. This collapse can be prevented by an on-line modulation of the amount of pheromone q which is laid down by ants. If the optimal regime is the one that maintains a collective choice for any flux values, then a high value of q at the beginning of the recruitment process when the flux is low would favor the emergence of the collective choice but it should decrease progressively as the flux increases. This seems to be the strategy adopted by ants *Lasius niger* (Beckers et al. 1992). Note the counter-intuitive trick of decreasing on-line the information left by each individual in order for the colony to maintain its choice.

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References

Anderson, C., & Franks, N. R. (2001). Teams in animal societies. *Behavioral Ecology*, *12*(5), 534–540.

Anderson, C., Franks, N. R., & McShea, D. W. (2001). The complexity and hierarchical structure of tasks in insect societies. *Animal Behaviour*, *62*(4), 643–651.

Ataya, H., & Lenoir, A. (1984). Le comportement nécrophorique chez la fourmi Lasius niger L. *Insectes Sociaux*, *31*, 20–33.

Beckers, R., Deneubourg, J. L., Goss, S., & Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Sociaux*, *37*, 258–267.

Beckers, R., Deneubourg, J. L., & Goss, S. (1992). Trail laying behaviour during food recruitment in the ant Lasius niger (L.). *Insectes Sociaux*, *39*, 59–72.

Beckers, R., Deneubourg, J. L., & Goss, S. (1993). Modulation of trail laying in the ant Lasius niger (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, *6*, 751–759.

Ben-Jacob, E., Schochet, O., Tenenbaum, A., Cohen, I., Cziròk, A., & Vicsek, T. (1994). Generic modelling of cooperative growth patterns in bacterial colonies. *Nature*, *368*(6466), 46–49.

Ben-Jacob, E., Cohen, I., & Levine, H. (2000). Cooperative self-organization of microorganisms. *Advances in Physics*, *49*, 395–554.

Beshers, S. N., & Fewell, J. H. (2001). Models of division of labor in social insects. *Annual Review of Entomology*, *46*(1), 413–440.

Bonabeau, E. (1996). Marginally stable swarms are flexible and efficient. *Journal de Physique I*, *6*, 309–324.

Bonabeau, E., & Theraulaz, G. (2000). Swarm smarts. *Scientific American*, *282*(3), 72–79.

Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S., & Camazine, S. (1997). Self-organization in social insects. *Trends in Ecology and Evolution*, *12*(5), 188–193.

Bonabeau, E., Theraulaz, G., & Deneubourg, J. L. (1998). Fixed response threshold and the regulation of division of labor in insect societies. *Bulletin of Mathematical Biology*, *60*, 753–807.

Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence—from natural to artificial systems*. Oxford: Oxford University Press.

Bruinsma, O. H. (1979). *An analysis of building behaviour of the termite Macrotemes subhyalinus*. Lanbouwhogeschool te Wageningen, The Netherlands.

Büchner, L. (1881). *La vie psychique des bêtes*. Paris: Reinwald.

Buhl, J., Gautrais, J., Solé, R. V., Kuntz, P., Valverde, S., Deneubourg, J. L., & Theraulaz, G. (2004). Efficiency and robustness in ant networks of galleries. *The European Physical Journal B—Condensed Matter and Complex Systems*, *42*(1), 123–129.

Buhl, J., Deneubourg, J. L., Grimal, A., & Theraulaz, G. (2005). Self-organized digging activity in ant colonies. *Behavioral Ecology and Sociobiology*, *58*(1), 9–17.

Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., & Simpson, S. J. (2006). From disorder to order in marching locusts. *Science*, *312*(5778), 1402–1406.

Burd, M. (2006). Ecological consequences of traffic organisation in ant societies. *Physica A: Statistical and Theoretical Physics*, *372*(1), 124–131.

Camazine, S., & Sneyd, J. (1991). A model of collective nectar source selection by honey bees: Self-organization through simple rules. *Journal of Theoretical Biology*, *149*(4), 547–571.

Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G., & Bonabeau, E. (2001). *Self-organization in biological systems*. Princeton: Princeton University Press.

Campos, M., Bonabeau, E., Theraulaz, G., & Deneubourg, J. L. (2000). Dynamic scheduling and division of labor in social insects. *Adaptive Behavior*, *8*(2), 83–95.

Chauvin, R. (1968). Sur le transport collectif des proies par Formica polyctena. *Insectes Sociaux*, *15*, 193–200.

Chauvin, R. (1971). Les lois de l'ergonomie chez les fourmis au cours du transport d'objets. *Comptes Rendus de l'Académie des Sciences de Paris D*, *273*, 1862–1865.

Couzin, I. D., & Franks, N. R. (2003). Self-organized lane formation and optimized traffic flow in army ants. *Proceedings of the Royal Society B Biological Sciences*, *270*, 139–146.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516.

Crichton, M. (2002). *Prey*. New York: HarperCollins.

Dambach, M., & Goehlen, B. (1999). Aggregation density and longevity correlate with humidity in first instar nymphs of the cockroach (Blattella germanica L., Dictyoptera). *Journal of Insect Physiology*, *45*, 423–429.

Deneubourg, J. L., & Goss, S. (1989). Collective patterns and decision making. *Ethology Ecology and Evolution*, *1*, 295–311.

Deneubourg, J. L., Pasteels, J. M., & Verhaege, J. C. (1983). Probabilistic behaviour in ants: a strategy of errors? *Journal of Theoretical Biology*, *105*, 259–271.

Deneubourg, J. L., Aron, S., Goss, S. A. P. J. M., & Duerinck, G. (1986). Random behaviour, amplification processes and number of participants: how they contribute to the foraging properties of ants. *Physica D*, *22*, 176–186.

Deneubourg, J. L., Goss, S., Pasteels, J. M., Fresneau, D., & Lachaud, J. P. (1987). Self-organization mechanisms in ant societies (II): learning in foraging and division of labor. In *Proceedings of the from individual to collective behavior in social insects conference* (pp. 177–196). Basel: Birkhäuser.

Deneubourg, J. L., Goss, S., Franks, N. R., Sendova-Franks, A. B., Detrain, C., & Chretien, L. (1991). The dynamics of collective sorting robot-like ants and ant-like robots. In *Proceedings of the first conference on simulation of adaptive behavior: from animal to animats* (pp. 356–365). Cambridge: MIT Press.

Deneubourg, J. L., Lioni, A., & Detrain, C. (2002). Dynamics of aggregation and emergence of cooperation. *Biological Bulletin*, *202*(3), 262–267.

Desneux, J. (1956). Structures "atypiques" dans les nidifications souterraines d'Apicotermes Lamani Sj. (Isoptera, Termitidae) mises en évidence par la radiographie. *Insectes Sociaux*, *V3*(2), 277–281.

Detrain, C., & Deneubourg, J. L. (1997). Scavenging by Pheidole pallidula: a key for understanding decision-making systems in ants. *Animal Behaviour*, *53*(3), 537–547.

Detrain, C., & Deneubourg, J. L. (2006). Self-organized structures in a superorganism: do ants "behave" like molecules? *Physics of Life Reviews*, *3*(3), 162–187.

Detrain, C., Natan, C., & Deneubourg, J. L. (2001). The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften*, *88*(4), 171–174.

Dorigo, M., Maniezzo, V., & Colorni, A. (1996). Ant system: optimization by a colony of cooperating agents. *IEEE Transactions on Systems, Man and Cybernetics, Part B*, *26*(1), 29–41.

Dorigo, M., Di Caro, G., & Gambardella, L. M. (1999). Ant algorithms for discrete optimization. *Artificial Life*, *5*(2), 137–172.

Dornhaus, A., Franks, N. R., Hawkins, R. M., & Shere, H. N. S. (2004). Ants move to improve: colonies of Leptothorax albipennis emigrate whenever they find a superior nest site. *Animal Behaviour*, *67*(5), 959–963.

Downing, H. A., & Jeanne, R. L. (1988). Nest construction by the paperwasp Polistes: a test of stigmergy theory. *Animal Behaviour*, *36*, 1729–1739.

Downing, H. A., & Jeanne, R. L. (1990). The regulation of complex building behavior in the paperwasp Polistes fuscatus. *Animal Behaviour*, *39*, 105–124.

Dussutour, A., Fourcassié, V., Helbing, D., & Deneubourg, J. L. (2004). Optimal traffic organization in ants under crowded conditions. *Nature*, *428*(6978), 70–73.

Dussutour, A., Deneubourg, J. L., & Fourcassié, V. (2005). Amplification of individual preferences in a social context: the case of wall-following in ants. *Proceedings of the Royal Society B Biological Sciences*, *272*, 705–714.

Forel, A. (1921). *Le monde social des fourmis du globe comparé à celui de l'homme*. Genève: Librairie Kundig.

Franks, N. R. (1986). Teams in social insects: group retrieval of prey by army ants (Eciton burchelli, Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, *18*, 425–429.

Franks, N. R. (1989). Army ants: a collective intelligence. *American Scientist*, *77*, 139–145.

Franks, N. R., & Fletcher, C. R. (1983). Spatial patterns in army ant foraging and migration: Eciton burchelli on Barro Colorado Island, Panama. *Behavioral Ecology and Sociobiology*, *V12*(4), 261–270.

Franks, N. R., Wilby, A., Silverman, B. W., & Tofts, C. (1992). Self-organizing nest construction in ants: sophisticated building by blind bulldozing. *Animal Behaviour*, *44*(2), 357–375.

Franks, N. R., Dornhaus, A., Fitzsimmons, J. P., & Stevens, M. (2003). Speed versus accuracy in collective decision making. *Proceedings of the Royal Society B Biological Sciences*, *270*(1532), 2457–2463.

Gadagkar, R., & Joshi, N. V. (1983). Quantitative ethology of social wasps: time-activity budgets and caste differentiation in Ropalidia marginata (Lep.) (Hymenoptera: Vespidae). *Animal Behaviour*, *31*, 26–31.

Gadagkar, R., & Joshi, N. V. (1984). Social organization in the Indian wasp Ropalidia cyathiformis (Fab.) (Hymenoptera: Vespidae). *Zeitschrift fur Tierpsychologie*, *64*, 15–32.

Garnier, S., Jost, C., Jeanson, R., Gautrais, J., Asadpour, M., Caprari, G., & Theraulaz, G. (2005). Aggregation behaviour as a source of collective decision in a group of cockroach-like robots. In *Proceedings of the 8th European conference on artificial life* (pp. 169–178), 5–7 September 2005. Berlin: Springer.

Gautrais, J., Theraulaz, G., Deneubourg, J. L., & Anderson, C. (2002). Emergent polyethism as a consequence of increased colony size in insect societies. *Journal of Theoretical Biology*, *215*(3), 363–373.

Gautrais, J., Jost, C., Jeanson, R., & Theraulaz, G. (2004). How individual interactions control aggregation patterns in gregarious arthropods. *Interaction Studies*, *5*(2), 245–269.

Gautrais, J., Michelena, P., Sibbald, A., Bon, R., & Deneubourg, J.-L. (2007, in press). Allelomimetic synchronisation in Merino sheep. *Animal Behaviour*.

Gordon, D. M. (1989). Dynamics of task switching in harvester ants. *Animal Behaviour*, *38*, 194–204.

Gordon, D. M. (1996). The organization of work in social insect colonies. *Nature*, *380*(6570), 121–124.

Goss, S., Aron, S., Deneubourg, J. L., & Pasteels, J. M. (1989). Self-organized shortcuts in the Argentine ant. *Naturwissenschaften*, *76*, 579–581.

Grassé, P. P. (1959). La reconstruction du nid et les coordinations inter-individuelles chez Bellicositermes Natalensis et Cubitermes sp. La théorie de la stigmergie : essai d'interprétation du comportement des termites constructeurs. *Insectes Sociaux*, *6*, 41–81.

Grassé, P. P. (1984). *Termitologia, Tome II. Fondation des Sociétés. Construction*. Paris: Masson.

Grünbaum, D., Viscido, S. V., & Parrish, J. K. (2005). Extracting interactive control algorithms from group dynamics of schooling fish. In *Proceedings of the cooperative control conference* (pp. 103–117). Heidelberg: Springer.

Haskins, C. P., & Haskins, E. F. (1974). Notes on necrophoric behaviour in the archaïc ant Myrmecia vindex (Formicidae: Myrmeciinae). *Psyche*, *81*, 258–267.

Helbing, D., Molnàr, P., Farkas, I. J., & Bolay, K. (2001). Self-organizing pedestrian movement. *Environment and Planning B: Planning and Design*, *28*(3), 361–383.

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge: Harvard University Press.

Howard, D. F., & Tschinkel, W. R. (1976). Aspects of necrophoric behaviour in the red imported fire ant, Solenopsis invicta. *Behaviour*, *56*, 157–180.

Jeanson, R., Ratnieks, F. L. W., & Deneubourg, J. L. (2003). Pheromone trail decay rates on different substrates in the Pharaoh's ant, Monomorium pharaonis. *Physiological Entomology*, *28*(3), 192–198.

Jeanson, R., Deneubourg, J. L., Grimal, A., & Theraulaz, G. (2004). Modulation of individual behavior and collective decision-making during aggregation site selection by the ant Messor barbarus. *Behavioral Ecology and Sociobiology*, *55*, 388–394.

Janson, S., Middendorf, M., & Beekman, M. (2005). Honeybee swarms: how do scouts guide a swarm of uninformed bees? *Animal Behaviour*, *70*(2), 349–358.

Jha, S., Casey-Ford, R. G., Pedersen, J. S., Platt, T. G., Cervo, R., Queller, D. C., & Strassmann, J. E. (2006). The queen is not a pacemaker in the small-colony wasps Polistes instabilis and P. dominulus. *Animal Behaviour*, *71*, 1197–1203.

Jost, C., Verret, J., Casellas, E., Gautrais, J., Challet, M., Lluc, J., Blanco, S., Clifton, M. J., & Theraulaz, G. (2007). The interplay between a self-organized process and an environmental template: corpse clustering under the influence of air currents in ants. *Journal of the Royal Society Interface*, *4*, 107–116.

Karsai, I., & Theraulaz, G. (1995). Nest building in a social wasp: postures and constraints. *Sociobiology*, *26*, 83–114.

Karsai, I., & Wenzel, J. W. (1998). Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proceeding of the National Academy of Sciences*, *95*(15), 8665–8669.

Kennedy, J., & Eberhart, R. (1995). Particle swarm optimization. In *Proceedings of the IEEE international conference on neural networks* (pp. 1942–1948). Washington: Bureau of Labor Statistics.

Krieger, M. J. B., Billeter, J. B., & Keller, L. (2000). Ant-like task allocation and recruitment in cooperative robots. *Nature*, *406*(6799), 992–995.

Kuntz, P., Snyers, D., & Layzell, P. (1999). A stochastic heuristic for visualising graph clusters in a bi-dimensional space prior to partitioning. *Journal of Heuristics*, *5*(3), 327–351.

Ledoux, A. (1950). Recherche sur la biologie de la fourmis fileuse (Oecophylla longinoda Latr.). *Annales des Sciences Naturelles et Zoologiques*, *11*, 313–409.

Lioni, A., Sauwens, C., Theraulaz, G., & Deneubourg, J. L. (2001). Chain formation in Oecophylla longinoda. *Journal of Insect Behavior*, *14*, 679–696.

Maeterlinck, M. (1927). *The life of the white ant*. London: Allen & Unwin.

Melhuish, C., Wilson, M., & Sendova-Franks, A. (2001). Patch sorting: multi-object clustering using minimalist robots. In *Proceedings of the 6th European conference on advances in artificial life* (pp. 543–552). London: Springer.

Menzel, R., & Giurfa, M. (2001). Cognitive architecture of a mini-brain: the honeybee. *Trends in Cognitive Sciences*, *5*, 62–71.

Moffett, M. W. (1988). Cooperative food transport by an Asiatic ant. *National Geographic Research*, *4*, 386–394.

Pankiw, T., Waddington, K. D., & Page, R. E. (2001). Modulation of sucrose response thresholds in honey bees (Apis mellifera L.): influence of genotype, feeding, and foraging experience. *Journal of Comparative Physiology A*, *187*(4), 293–301.

Parrish, J. K., Viscido, S. V., & Grünbaum, D. (2002). Self-organized fish schools: an examination of emergent properties. *Biological Bulletin*, *202*(3), 296–305.

Portha, S., Deneubourg, J. L., & Detrain, C. (2002). Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. *Behavioral Ecology*, *13*(6), 776–781.

Portha, S., Deneubourg, J. L., & Detrain, C. (2004). How food type and brood influence foraging decisions of Lasius niger scouts. *Animal Behaviour*, *68*(1), 115–122.

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T., & Franks, N. R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant Leptothorax albipennis. *Behavioral Ecology and Sociobiology*, *52*(2), 117–127.

Reeve, H. K., & Gamboa, G. J. (1983). Colony activity integration in primitively eusocial wasps: the role of the queen (Polistes fuscatus, Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, *13*, 63–74.

Reeve, H. K., & Gamboa, G. J. (1987). Queen regulation of worker foraging in paper wasp: a social feedback control system (Polistes fuscatus, Hymenoptera: Vespidae). *Behaviour*, *106*, 147–167.

Reynolds, C. W. (1987). Flocks, herds and school: a distributed behavioral model. *Computer Graphic*, *21*(4), 25–34.

Robinson, G. E. (1992). Regulation of division of labor in insect societies. *Annual Review of Entomology*, *37*(1), 637–665.

Seeley, T. D. (2002). When is self-organization used in biological systems? *Biological Bulletin*, *202*(3), 314–318.

Seeley, T. D., Camazine, S., & Sneyd, J. (1991). Collective decision-making in honey bees: how colonies choose among nectar sources. *Behavioural Ecology and Sociobiology*, *28*, 277–290.

Seeley, T. D., & Tautz, J. (2001). Worker piping in honey bee swarms and its role in preparing for liftoff. *Journal of Comparative Physiology A*, *187*, 667–676.

Seeley, T. D., & Visscher, P. K. (2004). Group decision making in nest-site selection by honey bees. *Apidologie*, *35*, 101–116.

Sudd, J. H. (1965). The transport of prey by ants. *Behaviour*, *25*, 234–271.

Sumpter, D. J. T., & Beekman, M. (2003). From nonlinearity to optimality: pheromone trail foraging by ants. *Animal Behaviour*, *66*(2), 273–280.

Theraulaz, G., & Bonabeau, E. (1995a). Coordination in distributed building. *Science*, *269*(5224), 686–688.

Theraulaz, G., & Bonabeau, E. (1995b). Modeling the collective building of complex architectures in social insects with lattice swarms. *Journal of Theoretical Biology*, *177*, 381–400.

Theraulaz, G., & Bonabeau, E. (1999). A brief history of stigmergy. *Artificial Life*, *5*, 97–116.

Theraulaz, G., Gervet, J., & Semenoff, S. (1991). Social regulation of foraging activities in Polistes dominulus Christ: a systemic approach to behavioural organization. *Behaviour*, *116*, 292–320.

Theraulaz, G., Gervet, J., Thon, B., Pratte, M., & Semenoff, S. (1992). The dynamics of colony organization in the primitively eusocial wasp Polistes dominulus (Christ). *Ethology*, *91*, 177–202.

Theraulaz, G., Bonabeau, E., & Deneubourg, J. L. (1998a). The origin of nest complexity in social insects. *Complexity*, *3*(6), 15–25.

Theraulaz, G., Bonabeau, E., & Deneubourg, J. L. (1998b). Response thresholds reinforcement and division of labor in insect societies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *265*, 327–332.

Theraulaz, G., Bonabeau, E., Nicolis, S. C., Sole, R. V., Fourcassié, V., Blanco, S., Fournier, R., Joly, J. L., Fernandez, P., Grimal, A., Dalle, P., & Deneubourg, J. L. (2002). Spatial patterns in ant colonies. *Proceeding of the National Academy of Sciences*, *99*(15), 9645–9649.

Theraulaz, G., Gautrais, J., Camazine, S., & Deneubourg, J. L. (2003). The formation of spatial patterns in social insects: from simple behaviours to complex structures. *Philosophical Transaction of the Royal Society A*, *361*(1807), 1263–1282.

Thorpe, W. H. (1963). *Learning and instinct in animals*. London: Methuen.

Traniello, J. F. A., & Robson, S. K. (1995). In W. J. Bell & R. Cardé (Eds.), *The chemical ecology of insects* (Vol. II, pp. 241–285). London: Chapman and Hall.

Tschinkel, W. R. (2003). Subterranean ant nests: trace fossils past and future? *Palaeogeography, Palaeoclimatology, Palaeoecology*, *192*(1–4), 321–333.

Tschinkel, W. R. (2004). The nest architecture of the Florida harvester ant, Pogonomyrmex badius. *Journal of Insect Science*, *4*, 21.

Vittori, K., Talbot, G., Gautrais, J., Fourcassié, V., Araujo, A. F. R., & Theraulaz, G. (2006). Path efficiency of ant foraging trails in an artificial network. *Journal of Theoretical Biology*, *239*, 507–515.

Weidenmüller, A. (2004). The control of nest climate in bumblebee (Bombus terrestris) colonies: interindividual variability and self reinforcement in fanning response. *Behavioral Ecology*, *15*(1), 120–128.

Wenzel, J. W. (1991). Evolution of nest architecture. In K. G. Ross & R. W. Matthews (Eds.), The social biology of wasps (pp. 480–519). Cornell University Press.

Wenzel, J. W. (1996). In S. Turillazzi & M. J. West-Eberhard (Eds.), *Natural history of paper-wasps* (pp. 58–74). Oxford: University Press.

Wilson, E. O. (1962). Chemical communication among workers of the fire ants Solenopsis saevisima (Fr. Smith): I. The organization of mass foraging. *Animal Behaviour*, *10*, 134–147.

Wilson, E. O. (1971). *The insect societies*. Cambridge: Harvard University Press.

Wilson, M., Melhuish, C., Sendova-Franks, A. B., & Scholes, S. (2004). Algorithms for building annular structures with minimalist robots inspired by brood sorting in ant colonies. *Autonomous Robots*, *17*(2), 115–136.

Wojtusiak, J., Godzinska, E. J., & Dejean, A. (1994). Capture and retrieval of very large prey by workers of the African weaver ant Oecophylla longinoda (Latreille). In A. Lenoir, G. Arnold & M. Lepage (Eds.), *Les insectes sociaux. 12th congress of the international union for the study of social insects* (p. 548), Paris, Sorbonne, 21–27 August 1994. Paris: Université Paris Nord.