

Review

Self-organized structures in a superorganism: do ants “behave” like molecules?

Claire Detrain *, Jean-Louis Deneubourg

Service d'Ecologie Sociale CP.231, University of Brussels, 50 avenue F.D. Roosevelt, B-1050, Brussels, Belgium

Received 24 July 2006; accepted 25 July 2006

Available online 27 September 2006

Communicated by L. Perlovsky

Abstract

While the striking structures (e.g. nest architecture, trail networks) of insect societies may seem familiar to many of us, the understanding of pattern formation still constitutes a challenging problem. Over the last two decades, self-organization has dramatically changed our view on how collective decision-making and structures may emerge out of a population of ant workers having each their own individuality as well as a limited access to information. A variety of collective behaviour spontaneously outcome from multiple interactions between nestmates, even when there is no directing influence imposed by an external template, a pacemaker or a leader. By focussing this review on foraging structures, we show that ant societies display some properties which are usually considered in physico-chemical systems, as typical signatures of self-organization. We detail the key role played by feed-back loops, fluctuations, number of interacting units and sensitivity to environmental factors in the emergence of a structured collective behaviour. Nonetheless, going beyond simple analogies with non-living self-organized patterns, we stress on the specificities of social structures made of complex living units of which the biological features have been selected throughout the evolution depending on their adaptive value. In particular, we consider the ability of each ant individual to process information about environmental and social parameters, to accordingly tune its interactions with nestmates and ultimately to determine the final pattern emerging at the collective level. We emphasize on the parsimony and simplicity of behavioural rules at the individual level which allow an efficient processing of information, energy and matter within the whole colony.

© 2006 Elsevier B.V. All rights reserved.

PACS: 87.18.Bb; 87.23.Cc; 87.23.Ge; 89.75.-k; 89.75.Fb; 89.75.Kd

Keywords: Self-organization; Decision-making; Pattern formation; Social insects; Foraging; Trail

Contents

1. Introduction	163
1.1. Self-organization and morphogenesis	163
1.2. Collective patterns in group-living animals	164
2. Scope of the review	164

* Corresponding author.

E-mail address: cdetrain@ulb.ac.be (C. Detrain).

3.	Part one: the ant society: a self-organized superorganism?	165
3.1.	A gallery of self-organized patterns	165
3.1.1.	Bifurcation	166
3.1.2.	Synchronization	167
3.1.3.	Self-organized waves	170
3.1.4.	Self-organized criticality: avalanche-like events	170
3.2.	Feed-back loops: the essence of self-organized structures	171
3.3.	Forming patterns through fluctuations	173
3.4.	Population size matters	173
3.5.	Sensitivity to environmental features	175
4.	Part two: why ant societies cannot be reduced to physicochemical systems?	177
4.1.	Ants tune system noise	178
4.2.	Simple rules and complex decisions: the use of “intelligent” criteria	180
4.3.	Ants estimate the number of conspecifics	182
5.	Conclusion	183
	Acknowledgements	184
	References	184

1. Introduction

1.1. Self-organization and morphogenesis

The natural world abounds in eye-catching structures such as the branching pattern of a slime mold, the regularity of a zebra coat or the synchronized movements of a fish school. Looking at the astonishing diversity and complexity of biological structures, people were tempted to understand the ins and outs of pattern formation. “Simple” explanations may attribute the complexity of patterns to some internal complexity of the genetic information encoded deep in the chromosomes. However, even though some basic elements of pattern formation are genetically coded, one can never easily nor straightforwardly relate the diversity of emerging structures to that of the genes themselves. In most cases, how a biological pattern is produced and what are the regulatory mechanisms involved often remain wide-open questions. As concisely pictured by Ball [5], “Once you start to ask the how of a mechanism, you are up against the rules of chemistry, physics and mechanics, and the question becomes not just “is the form successful?” but “is it physically possible?”. Such questions have led several researchers to build a bridge between physico-chemistry and life sciences. In this respect, the concept of self-organization which largely anchors its roots in the thermodynamics of irreversible processes proved to be very useful for the understanding of a variety of structures including biological ones (see e.g. [58]). At first, self-organizing processes were shown to produce striking patterns in the non-living world, such as the ripple marks on the surface of sand dunes, the hexagonal Bénard convection cells formed by heated oil or the swirling spirals of chemical compounds produced by Belousov–Zabotinsky reactions. All these examples share the same basic means by which they acquire their structure. Under a particular set of initial conditions and parameter values, patterns which extend well beyond the scale of their individual subunits, can arise spontaneously through physical and/or chemical interactions internal to the system, independently of any external ordering influence.

Today, the number of books or reviews dealing with self-organization applied to biology is continually expanding. They offer a fruitful multidisciplinary approach that highlights the major role played by self-organizing processes in the emergence of living structures, from cells to ecosystems (see e.g. [5,13,20,77,88,89,94,119]). This new approach substantially helps to characterize biological systems that possess emergent properties. The term “emergence” refers to a dynamic process by which the whole system acquires qualitatively new properties that cannot be foreseen from the simple addition of those of its individual components. Sudden transition from one pattern to another then arises suddenly from multiple non linear interactions between the living units. Such emerging structures are well known by embryologists who study how a homogeneous mass of cells suddenly becomes spatially organized so that cells will differentiate and the sequential process of development will progress. A first theoretical approach to self-organized morphogenesis is the pioneering work from Turing [128] who showed that a wide variety of biological patterns can spontaneously emerge out from a single mechanism, through the local amplification of a reaction (local activation)

and a long-range inhibition. Similar models were convincingly applied at the cellular level. For example, they account for the segmentation of insect embryos [78] or for the formation of complex pigmented cell patterns such as those observed on shells [88,89], butterfly wings or leopard coats [92,93]. All these patterns adhere to a general theme and rely on the same local activation-long range inhibition mechanism. The diversity of those patterns depends on simple changes in parameter values such as the time at which the mechanism is activated or the geometry of the animal. A last fascinating convergence in pattern formation is found out at the higher level of ecosystems such as the regular striped patterns of bushes in savannahs [81] or the periodic outbreaks of insect population density (for a review see [94,127]). Although quite different in scale and function, all these biological structures share the common property of being self-organized. None would pretend that self-organizing processes fully account for all the details and steps in the formation of these specific patterns. Nonetheless, they offer a fair representation of some major mechanisms shaping nature and show how comparatively easy it is to generate diversity at different levels of the living world.

1.2. Collective patterns in group-living animals

Animal societies display some of the most impressive biological structures of which the understanding has been a major challenge for generations of scientists. Despite they are complex assemblages of individualities who behave depending on their own and sometimes conflicting interests, group members may respond to their environment in a highly coordinated way. Spatial patterns emerge even within groups of several hundredths of individuals such as the amazing collective movements of insect swarms, fish schools, bird flocks or mammals' herds [28,98,99]). Besides, group activities can be structured through time such as the well-known synchronized flashing of fireflies [115], for a review on biological rhythms see [59,136]. In the past decades, the question of how such order arises among group-living animals became fundamental to fully understand the sociality phenomenon. Unexpectedly, many of those collective behaviour that were selected throughout evolution, emerge simply from interactions between group members, even when there is no directing influence imposed by an external template, a pacemaker or a leader [20]. In other words, animal societies turn out to be replete with patterns that exhibit organization without an organizer, coordination without a coordinator. Self-organization (SO) even alters common beliefs about the origin of highly complex structures such as hierarchy in primate societies which ranges from “despotic” to “egalitarian” social systems [122]. In “despotic” primate species, benefits such as priority of access to mates, food and safe spatial locations, are strongly biased towards higher-ranking individuals while in “egalitarian” species access to resources is more equally distributed. It is suggested that the numerous behavioural differences between egalitarian and despotic macaques automatically emerge within the society and can be traced back by simple differences in group-members interactions (e.g. in: the intensity of aggression or the tendency of monkeys to support related individuals [70]).

By including self-organization into classical questions of ethology and sociobiology, the diversity of social structures can now be explained without assuming complex behaviour as well as high cognitive abilities at the level of the individuals. One may become very enthusiastic by thinking about collective phenomena in this way since self-organization is a parsimonious way to capture much though certainly not all of the real complexity of animal societies. Such approach is not a search for simplicity for simplicity's sake but, instead, it meets one of sciences' guiding principles—the Ockham's razor—demanding an economy of hypotheses for problem-solving and favouring simpler explanations at the expenses of complicated ones. Heuristic though the self-organization paradigm may be, one should however keep in mind its limits since specific problems arise as one studies a population of living organisms. Animals, unlike molecules, are autonomous units which are socially differentiated: depending on its genetic background and life experience, each individual differs from another in the ways it will react to stimuli or tune its interactions with other group members. Unlike physico-chemical units which passively “undergo” the shaping effect of SO, social differentiation coupled with a relatively high autonomy of each living unit may enhance or counteract the impact of self-organizing processes on the group structure. Ultimately, an animal species should “conciliate” those individual specificities with the ability to produce at the colony scale a coordinated response that will be adaptive and retained throughout the evolution.

2. Scope of the review

Among group-living animals, ants provide us with a kaleidoscope of emerging patterns and with a unique model to relate every facet of social organization to life histories, ecological or evolutionary issues. Through examples taken

from the world of ants, we will explore the benefits but will also stress on the limits of applying a SO approach to social structures. In the first part of this review, we will show how self-organization captures a part of the diversity of ants' social patterns. We shall start with a survey of spatio-temporal structures in ant societies which are analogous to self-organized patterns observed in physical and biochemical systems. Among this gallery of "myrmecological" patterns, foraging ones provide many impressive examples and will be therefore our guiding thread to examine several properties which are typical signatures of self-organization. We will show how fluctuations, colony size and environmental parameters act upon the dynamics of feed-back loops between interacting nestmates and hence shape the collective response of the whole ant society. Nonetheless, the impressive structuring role of self-organization should not give us a naïve and misleading feeling of having caught the complexity of ant social patterns. Therefore, the second part of the review will aim at providing a cautionary advice about making physics with too little of biology. Each animal individual is in itself a complex entity and the very understanding of pattern formation in social insects needs to go beyond a simplistic "molecular" description of ants' behaviour: We will emphasise on the ability of each ant to process information and to accordingly tune its interactions with nestmates as well as on the functional properties of social patterns. In this respect, we will demonstrate that, beyond simply forming patterns, social insects solve problem and take decisions that act upon the processing of both information and matter within the whole colony and that determine the efficiency of energy flow or communication between group members.

3. Part one: the ant society: a self-organized superorganism?

Insect societies are commonly seen as the best-achieved paradigm of social life. Like bees or termites, ants are famous for their striking organization and highly efficient responses to everyday challenges [72,111]. Due to the high integration level of nestmates, the term "superorganism" has historically gained wide use when referring to those societies. Likewise any metazoan, ant societies are made of units that are differentiated into sterile or reproductive individuals and function as a cooperative unit. Yet the analogy is clearly strained since somatic cells are all genetically identical while ants are not. Due to the haplo-diploïdic system of reproduction in ants, the level of genetic relatedness between nestmates is usually high and can reach up to $r = 0.75$ (e.g. in humans $r = 0.50$ between brothers/sisters). Due to this high kinship relatedness, ants behave to maximize not only their own direct fitness but also that of nestmates in the whole colony (indirect fitness) [91,131,132]. One biological feature of ant superorganism is of particular interest for the present review that is the ability of a large number of nestmates to function as a whole and to take collective decisions. Embedded in the existence of a highly structured organization is the common—but erroneous—belief of a social leader such as the queen centralizing information and issuing commands to workers. Instead, the removal of presumed leading individuals reveals that spatio-temporal patterns still persist and thus essentially rely on interactions among nestmates or between nestmates and their environment. Without having a sense of the whole, the worker individuals collectively behave and solve daily problems such as exploration of new areas, foraging, nest moving, nest defence, waste management or brood care (for a review see [20,72]). The next sections provide a brief survey of ant patterns showing strong analogies and properties with that of SO patterns in physico-chemical systems.

3.1. A gallery of self-organized patterns

In physico-chemical or biochemical systems, a wide array of patterns can appear spontaneously in an initially homogeneous medium without any external driving force or influence. Likewise, ant patterns may change abruptly and orient spontaneously to one of them depending on fluctuations and initial conditions. From a practical point of view, the identification of self-organizing processes in ant societies ideally requires a two-ways approach coupling behavioural experiments and modelling. Therefore, non-linear models have been developed in which agents are designed to behave similarly to animal individuals [94,118]: they act in a probabilistic way, respond exclusively to the local information they receive from their nearby environment and follow simple decision rules coupled with feed-back loops (for further details see next sections). The level of agreement between actual and such model-predicted collective behaviour indicates the prevalence of self-organizing processes in pattern formation. However, specifically designed experiments coupled with modelling are not so common in socio-biological literature. Table 1 lists all ant patterns in which a strong self-organizing component was identified—or at least highly suspected to occur—and indicates the presumed mode of interaction responsible for the emergence of such structures.

Table 1
Self-organized patterns in ant societies

Category	Self-organized patterns	Type of interaction	Ant species	References	
Bifurcation	Transition between disordered and ordered pattern	Chemical: trail pheromone	<i>Monomorium pharaonis</i> <i>Pheidole pallidula</i>	[9,42]	
	Transition from an even use to a selection of one food source only	Chemical: trail pheromone	<i>Lasius niger</i>	[32,100]	
	Formation of branched nest galleries	Chemical: digging pheromone	<i>Lasius niger</i> <i>Messor sancta</i>	[17,18,103]	
	Collective choice of one exit by escaping ants	Unknown	<i>Atta insularis</i>	[1]	
	Chain formation	Mechanical: mutual grasping of legs	<i>Oecophylla longinoda</i>	[35]	
Synchronisation	Short rhythms scale (min)	Alternation of activity/resting periods within the nest	Mechanical: mutual activation through physical contacts	<i>Camponotus planatus</i> <i>Tapinoma litorale</i> , <i>Pseudomyrmex cubaensis</i> , <i>Monomorium floricola</i> several <i>Leptothorax</i> species	[12,23,25,51]
Self-organized waves	Alarm waves	Mechanical: mutual activation through physical contacts	Argentine ant species: <i>Linepithema humile</i>	[67]	
	Rotating trails	Spatial changes in food resources acting on trail laying activity	Harvester ant: <i>Messor pergandei</i> Army ants: <i>Eciton burchelli</i>	[52,64,65,105]	
Self-organized criticality	Abrupt changes in number of feeding ants	Mechanical: mutual activation through physical contacts	Argentine ant species <i>Linepithema humile</i>	[66]	
	Formation of ants' "droplets"	Mechanical: mutual grasping & gravity	<i>Linepithema humile</i>	[120]	

3.1.1. Bifurcation

Non-linear systems consisting of simple interacting units often exhibit multiple states. Most physicists consider as a typical signature of self-organization, the occurrence of a bifurcation which is the abrupt transition of the entire system towards a new stable pattern when a threshold is crossed. For example, at a critical temperature, a ferromagnet may become demagnetized due to the disordering effect of thermal forces. Upon variations of some control parameters, a self-organized system will thus spontaneously present new types of structures whereby there is a discrete change from one state to another. As regards biological sciences, the possibility of such discrete changes is namely at the root of current views about speciation and morphological diversification in which dynamic processes of development take place in a sequential way with each step bifurcating from a previous one. Similar bifurcation phenomena are observed in ant societies which may abruptly shift from a disordered to an ordered pheromone-based foraging [9] or from a random exploration to a well-defined exploratory trail [42]. Bifurcation may take the form of symmetry-breakings as one observes the shift from an even exploitation of several food sources or an equal resting in several sites towards the collective exploitation of only one food site or the selection of a specified resting location. One should underline that in social systems such symmetry-breaking does not necessarily evoke to biologists a SO script as they can put alternative explanations forward. Among those alternatives, the coordinated movement towards a restricted area can be driven by one or a few leaders that are merely followed by nestmates or the collective choices can result from environmental

heterogeneities in which each group member decides on its own to move towards the more “hospitable” place. In both cases, there is no self-organizing mechanism, no amplifying interactions at work nor assumptions of non-linearity. As soon as the existence of leaders or of environmental templates are dismissed, SO can be evoked as the main process leading to these symmetry-breakings.

Experimentally, there is a simplistic way to visualize a bifurcation by confining ant foragers to a diamond-shaped bridge of which each equally long branches lead to a sucrose solution. At the beginning, starved ants evenly explore both branches of the bridge. After a while, a bifurcation occurs so that most of the foragers travel over one path only (Fig. 1(a)). Such examples of collective choice have been reported for a wide variety of ant species which recruit nestmates towards new food resources by the laying of a chemical trail [32,118]. The basic scheme of interactions is similar for all these species and can be described as follows (Fig. 2). As soon as one ant has succeeded in discovering a food source, it goes back to the nest and lay a chemical trail. The trail pheromone then triggers the exit of additional foragers and guides them as an Ariane thread to the food source. After feeding, each recruited ant can in turn reinforce the foraging trail and stimulate other nestmates to forage. This trail reinforcement results in a non-linear increase of foragers’ population which can lead to a self-organized bifurcation and the exploitation of one single food source (for further details on the formation of bifurcation see also Section 3.2 of this review). One should bear in mind that a discretized environment (e.g. diamond-shaped bridge) is a quite convenient way to visualize bifurcation but is far from natural conditions. In a more continuous environment, symmetry breakings will rather occur in a cascade leading to the emergence of a branched network of foraging trails.

Bifurcation and symmetry-breakings are features common to a variety of ants’ collective behaviour. For example, in panic conditions, ants confined to a cell with two symmetrically located exits, prefer to escape through one of the exits if alarm is created by adding a repellent fluid [1]. Likewise when emigrating, weaver ants will shift from an even distribution to a spatial concentration and a self-assembling of tenths of workers into chains at only one location [35]. In the context of nest building, the topology of underground galleries—which varies from a tree-like structure to a highly connected tunnelling network—results from a dynamics of excavation which is clearly non-linear and from several bifurcation events [17,18]. The probability for an ant to dig out a sand grain increases in places where other ants had previously dug, leading to the formation of new bifurcations along extending galleries and to the selection of one digging site among the several initiation sites that were first randomly excavated [103].

3.1.2. Synchronization

Although living systems are complex, they can be highly ordered in time. There is a plethora of biological oscillations such as the periodic firing in neurons, the biochemical cycle of glycolytic pathway, the life cycle of the cellular slime mold or the coupled oscillations of populations of preys and predators [59,115,136]. All the above examples are different from biological clocks associated with circadian or daily rhythms. They are not periodic by virtue of some external periodic forcing function and they can be reasonably described as autonomous oscillators.

Temporal patterns also exist in ant societies: oscillatory processes appear in widely varying contexts and can have periods from a few seconds to hours and even days and weeks. Recent studies found out that activity rhythms occur over short time scales, activity being defined here as movement of any type within ant colony [12,23,25]. Indeed, the average daily activity of nestmates is neither constant nor random but displays periodic bursts: one ant initially becomes active, and then activity spreads to neighboring workers before gradually dying out. Fourier analyses of activity patterns in these colonies reveal periodic components with activity peaks occurring at regular time interval [51] (Fig. 1B). Since nature provides many types of pacemakers such as diurnal light-dark cycles, one may first think about external stimuli to explain such a rhythmic activity. However, it was shown that synchronized activity within ant colonies can emerge simply from mutual activation through direct physical contacts. Active ants are effective in stimulating inactive ones without an exogenous trigger. The periodicity of colony activity relies either on ants remaining active for a minimum time [113] or on active workers becoming quiescent for a refractory period during which they cannot be reactivated [63]. The fundamental outcome of this autocatalytic process is that individuals become rhythmic as a group, even though they show no intrinsic rhythm. Such synchronization could be adaptive when several active workers are required for a task (e.g. foraging, brood care, defense or nest building) to be performed efficiently, although this explanation has still to be experimentally validated.

Temporal patterns may also occur over long time scale such as the periodic alternation of static and nomadic phase in colonies of army ants. During the static phase, the queen lays thousands of eggs in a brief span of time, within a few days, and the colony remains in one bivouac site. When pupae derived from the previous batch of eggs develop

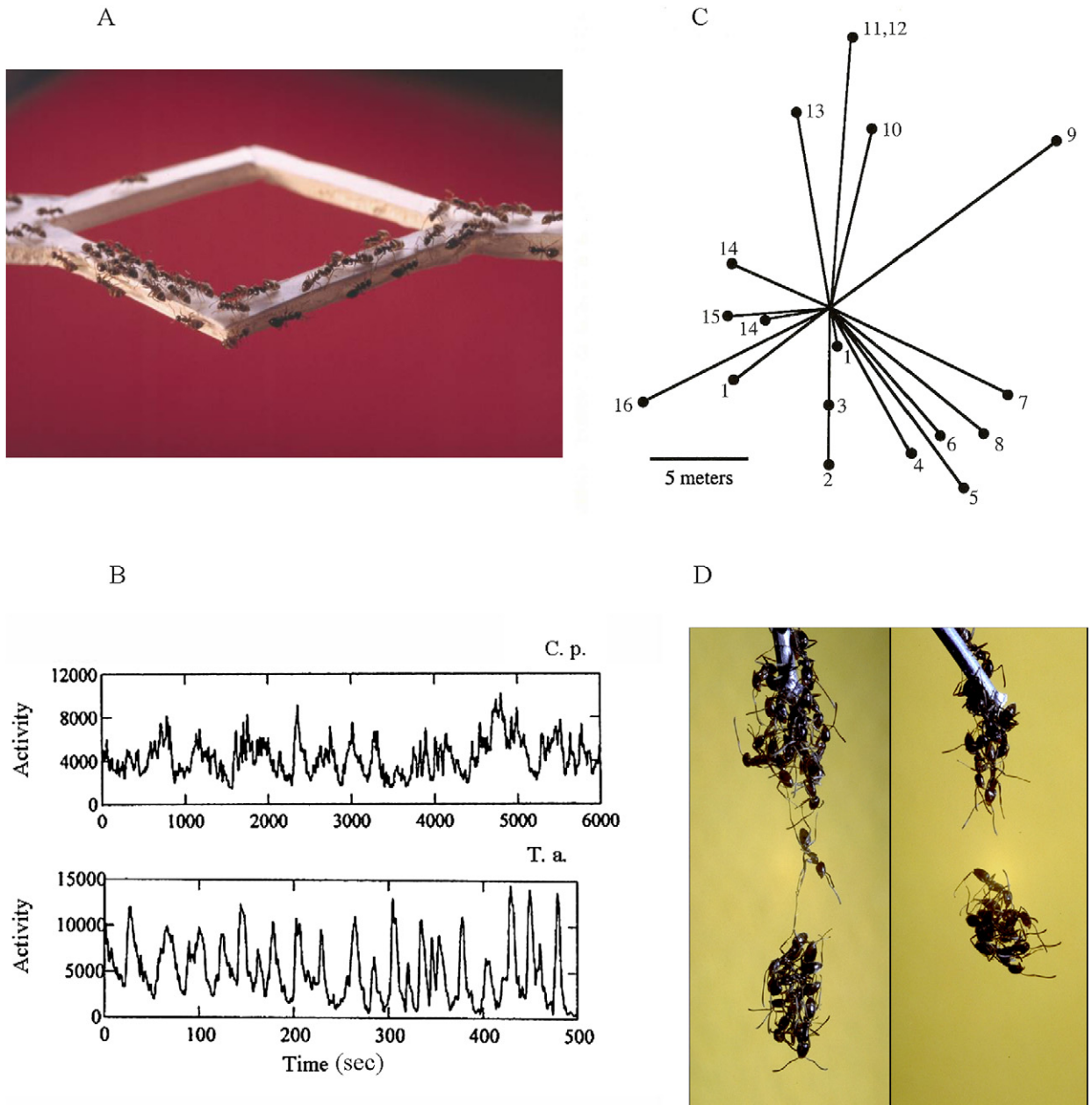


Fig. 1. Self-organized patterns in ant societies. (a) Symmetry-breaking: collective selection by all *Lasius niger* workers, of one foraging path over a diamond-shaped bridge leading to one food source. ©CNRS Photothèque/VIDAL Gilles. (b) Periodic bursts of activity of two ant species. The y-axis is activity measured in pixel changes between successive images of ants' location within the nest and the x-axis is time in 5-s intervals for *Camponotus planatus* (C.p) and in 30 s intervals for *Temnothorax (Leptothorax) allardycei* (T.a) (redrawn from Cole & Trampus [25]). (c) Rotating trails of the harvester ant *Messor pergandei*. The numbers identifying each trail refer to their sequential observation over foraging time (based on Rissing & Wheeler [105] data). (d) Droplet of clustered Argentine ants *Linepithema humile* falling down as a critical number of workers is reached. ©CNRS Photothèque/Theraulaz Guy.

into adults, the appearance of tens of thousands of new workers induces an increase in the general activity level as well as in the intensity of swarm raids. Then, the colony enters a nomadic phase during which it starts emigrating at the end of each day's foraging. The migratory phase continues as long as brood remains in the larval stage. As soon as they pupate, the emigration stops and a new static phase begins. This remarkable periodic behaviour is truly endogenous: it is not linked to any weather event and continues at the same tempo over years. Instead, the activity

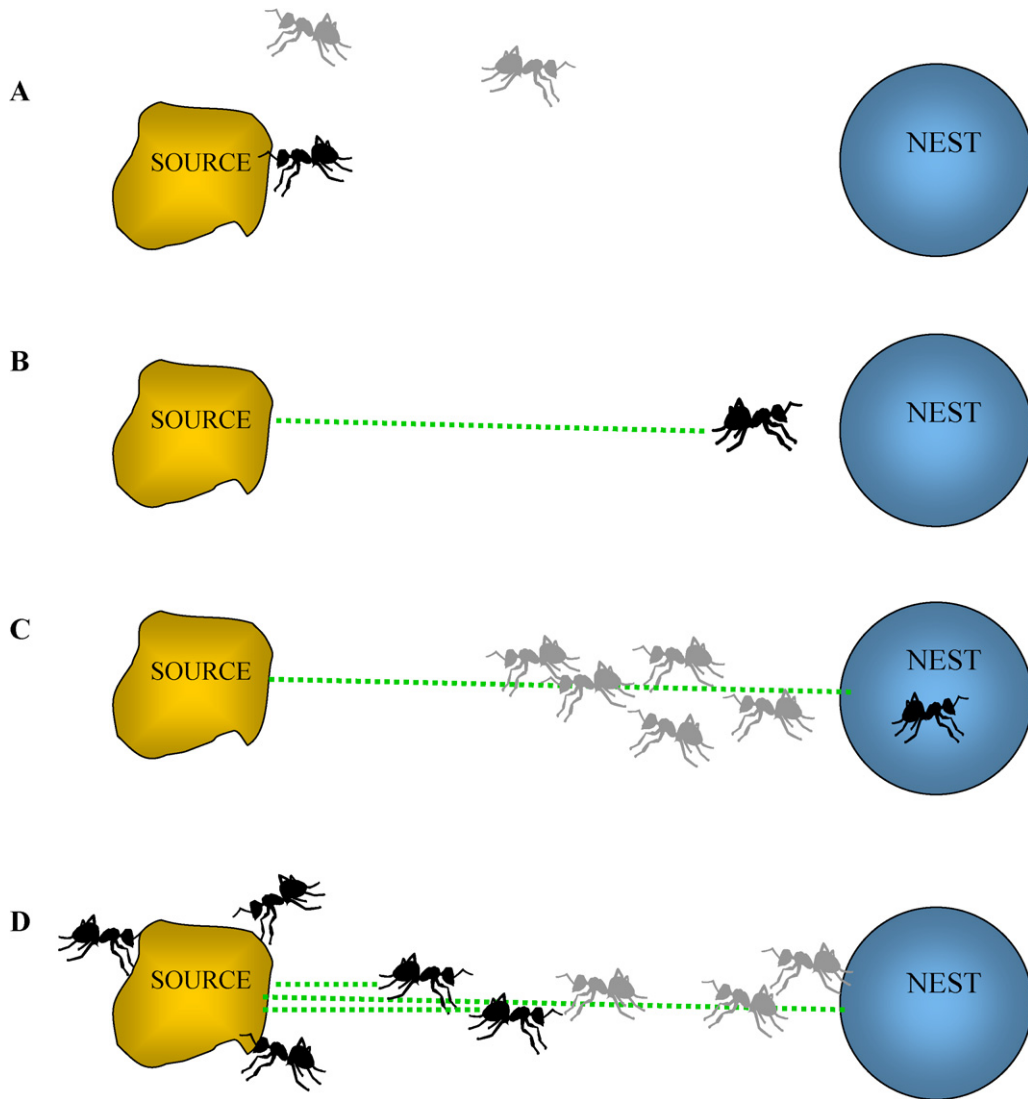


Fig. 2. Trail recruitment in ants. An ant scout (in black) which has found a food source (a), lays a pheromone odor trail on its way back to the nest (b). The recruitment trail is then perceived by nestmates (in grey) which exit the nest and follow the trail till they reach the food source (c). In turn, these recruited workers feed at the source and return to the nest reinforcing the foraging trail (d).

cycle seems to be controlled by periodic changes in larvae stimuli coupled with the reproductive physiology of the queen as follows. The laying by the queen of all her eggs in one brief burst is responsible for the synchronisation of egg hatching, larvae development as well as emergence of callow workers. Due to the concurrent hatching of eggs, the steep increase in larval needs drastically reduces food supply to the queen as well as its fecundity. In addition, larvae food demand stimulates workers to search for resources over extended distances as well as to enter into a nomadic phase by performing regular nest moving towards new foraging areas. As larvae grow old and become non-feeding pupae, the resulting abrupt decrease in food demand and foraging activity allows the colony to exploit a more restricted area and to settle down into a static phase. Moreover, the extra food amount is available for the feeding of the queen of which egg-laying activity is re-boosted leading to the release of a new large batch of eggs within a few days [110]. Such synchronization is thus based entirely on physiological and behavioural mechanisms that are internal to the social system. Likewise, a phylogenetically related species [104] displays a reproductive cycle in which two phases of adult activity alternate in synchrony with the brood instars. Again, the onset of cyclic activities is endogenous and triggered by larvae-induced excitement rather than by external factors or pace-makers inbuilt in adult ants.

3.1.3. Self-organized waves

The Belousov–Zhabotinsky reaction is one of the prominent examples of nonlinear dynamical patterns in chemistry. In this reaction, an organic substrate (malonic acid) is oxidised by an acidified bromate solution. In a 2D set-up, waves propagate as rings of oxidation which form target patterns. The heart of this propagation is the autocatalysis of the intermediate HBrO_2 (bromous acid) and the propagation velocity of the front depends on the reaction rate and the diffusion constant. When the pattern is disturbed, it is possible to observe spiral waves [135].

Beside the Belousov–Zhabotinsky reaction which is probably the most widely known example of self-organized wave [135], there is a vast number of phenomena in biology where a key element to pattern formation seems to be a travelling wave either of chemical concentration or of mechanical deformation. For example, wave-like phenomena appear in a developing embryo after egg fertilization or within a population of cells when spatial effects are important such as in the periodic aggregation waves of *Dictyostellium discoideum* amoebae [59,136]. During their development, amoebae cells communicate over distances by periodically producing the chemo-attractant cAMP. This signal propagates outward, away from an aggregation centre by using a relay system of cAMP-induced synthesis and secretion of cAMP by surrounding cells and concurrently triggers waves of chemotactic movements among amoeba population in the direction of the aggregation centre [59,124]. Wave-like events were scarcely reported in ant societies, probably due to the difficulty for experimentalists to follow spontaneous displacements of activity at both temporal and spatial scales. Alarm waves were nevertheless described in Argentine ants. If a threshold number of ants (10 to 20 feeding ants) are disturbed, an alarm wave is initiated and propagates rapidly within the group [67]. Likewise, in the dwarf honeybee, foragers which perceive a potential threat to the colony, emit a warning signal (piping) audible to the human ear which is transmitted through the comb and which initiates less than one second later a collective acoustic response (hissing) by a significant number of colony members. Hissing begins in individuals close to the piping bee, spreads as a wave to the neighbours in a coordinated crescendo that might serve as a deterrent to small predators. Communication of risk through such travelling waves is presumably rapid and thus beneficial if a significant danger is detected [109].

Waves of activity can also take the form of periodic changes in the spatial distribution of foragers. For example, in army ants, although the swarm maintains a given direction of progress, it turns first to one side and then to the other in swings of 15° to 25° like an ever-extending pendulum [110]. Over longer time scale, the daily radial displacement of main trails—so called rotating trails—provides another example of a travelling wave. In *Eciton burchelli*, a new swarm raid develops each day out of the nest: aroused workers start exiting the bivouac, expanding in all directions and soon, one sector becomes favoured by all raiders that enter new ground. As regards their direction, the successive raids rotate about the bivouac site systematically so that foraging overlap between successive days was minimized ([52,65] but see also [110]). Likewise, a spectacular radial displacement of foraging trails was observed in some harvester ant species (Fig. 1(c)). Indeed, the main foraging trail makes a more or less complete revolution by rotating with a period of several days to three weeks around the nest entrance like the hand of a clock [105]. A mathematical model shows that this self-organized clock pattern can be generated from the concurrent effects of trail-laying foragers which recruit nestmates and of the environment which becomes locally depleted of food resources around the foraging column [64]. Wave-like events in the swarms of army ants or in the foraging columns of harvester ants confirm that self-organized movements are more structured—both spatially and temporally—than could be expected in the absence of leaders or centralized control.

3.1.4. Self-organized criticality: avalanche-like events

Disturbance patterns may occur within a group of ants and show striking similarities with disturbances reported in self-organized critical systems—also called “avalanches” [4]. For instance, as a sand pile grows by the slow addition of individual sand grains at random position, the slope become steeper up to a critical value. If more sand is added, it is likely to slide off and to trigger an avalanche whose size is given by the number of sliding grains. The power law $f \sim x^{-a}$ that describes the frequency f of avalanche size x is considered as the signature of a self-organized criticality.

Similar endogenous disturbances were described within a population of Argentine ant workers feeding at a food source. Without any external disturbance, a transient departure from the food source can be triggered by an initial contact between a wandering ant and feeding nestmates [66]. Likewise, under certain experimental conditions, an aggregate of Argentine ant workers may form at the end of a rod and a droplet of around 40 ants may fall down without any external disturbance (Fig. 1(d)). When the flux of incoming ants is sufficiently high, this process of droplets’ fallings can continue for hours [120]. The magnitude of these displacements (i.e. in the number of leaving or

dropping ants) broadly follows a power law distribution characteristic of self-organized critical systems. These abrupt changes in the size of groups of ants fit well to avalanche models and are quite similar to the observed criticality of sand piles [76]. Although these disturbances may reduce food exploitation because foraging ants are interrupted, they could give to ants' group the advantage of rapid alarm communication and escape behaviour.

These analogies between physico-chemical and social patterns strongly suggest that self-organizing processes shape many life-sustaining activities of social insects. Nevertheless, few studies overcome the descriptive level and provide a quantitative and heuristic approach to pattern formation in ant societies. The best-achieved research in this field concerns the formation of foraging patterns. Indeed, the sight of hundredths of ants moving together in raiding swarms or following accurately a trail network till a restricted food area while neglecting other nearby food sources has easily prompted the “how” question among researchers. Therefore, key-properties of self-organizing systems will be addressed in the next section of this review through case examples exclusively drawn from ant foraging context, even though our conclusions apply to other social structures and group-living organisms.

3.2. Feed-back loops: the essence of self-organized structures

Many physico-chemical patterns are well-known to appear spontaneously when competing driving forces banish featureless uniformity. Likewise, two opposite types of interactions among group members—positive and negative feed-backs—both contribute to the emergence of social structures. It is widely recognized that the identification as well as the understanding of these feed-back mechanisms provides a key to understanding how insect societies display complex collective patterns and organize their workforce efficiently.

As regards positive feed-backs, various forms are encountered among group members that can often be reduced to the rule of thumb “Do as your neighbor”. In particular, information-laden signals can release a specific behavioural response in the receiver which may, in turn, produce a signal identical to the one he received. Such positive feed-back loop will ultimately lead to the propagation and amplification of information and/or behaviour. In the case of ant foraging, positive feedbacks often take the form of pheromone trails deposited by ants that have found a profitable food source (Fig. 2). Social amplification through the laying of a recruitment trail can be easily evidenced in a Y-shaped setup in which ant foragers have the choice between two branches of equal length each leading to a food source [Fig. 3, [7,30,117]]. The probability of choosing one branch 1—here called p_1 —at a certain time depends on the number of ants having already laid a trail on this branch 1 and can be described by the following equation:

$$p_1 = \frac{(x_1 + \alpha)^\beta}{(x_1 + \alpha)^\beta + (x_2 + \alpha)^\beta}, \quad p_2 = 1 - p_1 \quad (1)$$

in which x_i is the amount of pheromone on branch i , α determines the attraction level of an unmarked branch and β accounts for the nonlinearity of the choice function (in the case of *L.niger* species; $\beta \sim 2$). Positive feed-backs by trail pheromone are nonlinear in that ants do not react in a proportionate manner to the amount of pheromone deposited. Instead, strong trails elicit disproportionately higher probabilities that newly coming ants will choose and reinforce them than weak trails. This positive feed-back eventually leads to a bifurcation—meaning the selective exploitation of only one resource or the selective use of only one path (Fig. 3 see also Fig. 1A).

As regards negative feed-backs, beyond simply forcing a process to stop, they keep amplification under control, tune the recruitment dynamics and help to shape it into a particular pattern (for a review see [43,72,134]). A first set of negative feed-backs are directly related to the limited size of ant population available to participate in a given activity (e.g. the limited population of potential recruits). As a result, the initial snowballing effect of recruitment trail usually gives way to a phase in which further growth is self-inhibited. This leads to a typical logistic dynamics starting by an exponential growth phase followed by a plateau value. Furthermore, a cross-inhibition occurs between concurrent trails since the growth of one trail automatically reduces the number of foragers still available to follow the other path. A second set of negative feed-backs are given “for free” by the environment and automatically result from the own activity of the insects. Inhibition can arise from physical constraints at the food source (e.g. overcrowding or food depletion) or within the nest (e.g. filling of food reserve). A decreased response to recruiting stimuli can also result from physiological limitations (e.g. a satiation of workers) (Fig. 3). Finally, some experimental results suggest that the amplification can be actively offset by ants which either follow “keep-away” behavioural rules or emit negative trail pheromones [106]. Simulations demonstrate that the effectiveness of foraging is actually improved if negative trail pheromone is used as a “no entry” signal repelling ants from an unrewarding route [114].

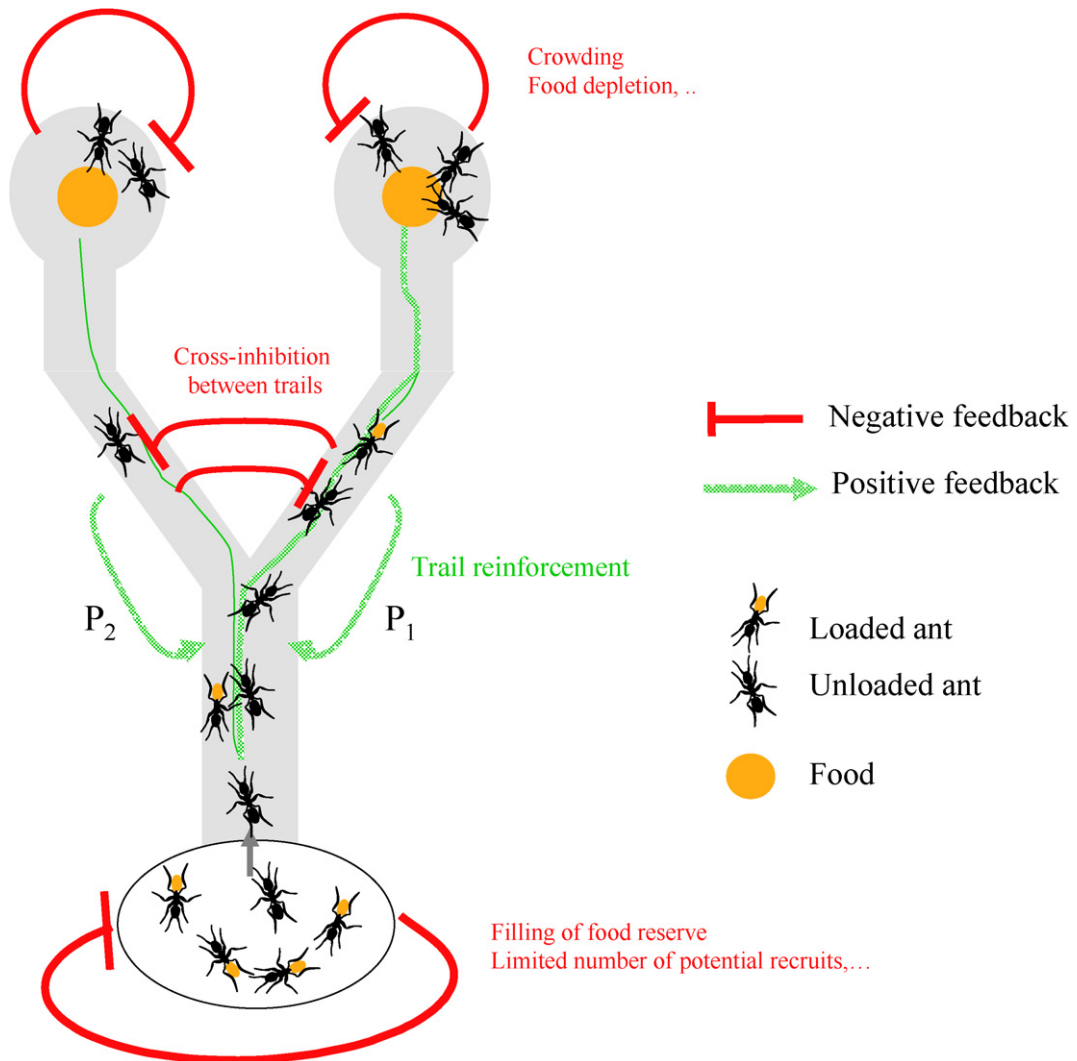


Fig. 3. Feed-backs loops and collective choice of one food source (bifurcation). When two food sources of equal quality are offered to an ant society, only one becomes selected through the concurrent influence of positive (in green) and negative (in red) feed-back loops. Examples of such feed-backs are given in the figure and further detailed in the text. Depending on these feed-backs, the trail amount and hence the probability for newly coming ants to choose one path (either P_1 or P_2) at the bifurcation point will change over time (see Eq. (1) in text) and will ultimately lead to the collective choice of one food source. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A wide array of large-scale patterns (see examples listed in Table 1) have such feed-back loops built into them which either activate (positive feed-backs) or inhibit (negative feed-backs) the production of a signal or the releasing of a behaviour. Likewise, several spatial structures outcome from the coupling of autocatalysis (short-range activation) with self-inhibition (long range inhibition). For instance, the spatial organization of ant clusters within the nest or the formation of cemeteries results from antagonist feed-backs: the resting of ants or the addition of corpses to a cluster becomes more likely as the cluster increases in size but is inhibited by the depletion of ants or corpses in the cluster neighbourhood [34,38,121]. The building behaviour of ants also provides us with another clear example in which a collective pattern results from opposite feed-backs loops. While excavating, the insect adds pheromone to the cavity walls and the laid pheromone, in turn, stimulates other nestmates to dig at that site. As the nest volume increases, the density of insects and so the frequency of their visits to the digging sites decrease what ultimately leads to a self-regulation of the excavated nest volume [17,18,103].

For years, the experimental identification of these feed-backs has been hindered by a number of practical difficulties. Now, models and simulations which are often based on a rather simple mathematical formalism help to validate hypotheses about the relative contribution of each feed-back mechanism into the emergence of a global structure [14, 20, 116, 118]. These studies based on both an experimental and a theoretical pillar confirm that, in many aspects of social life, the very essence of spatial structures and activity patterns relies on the coupling of positive and negative feed-back loops. Most of the positive feed-backs are genetically coded behaviours (e.g. the production of a recruitment signal) and promote the creation of collective structures while, in contrast, negative feed-backs often arise as automatic by-products of the ants' activity and help to stabilize the collective pattern.

3.3. *Forming patterns through fluctuations*

In non-linear systems, fluctuations at the unit level, even small ones, can lead to the deep changes at the global level so that the whole system will reach one of its multiple stable states [49, 130]. For instance, out of a disordered phase, liquid crystals may adopt a structured positioning into parallel alignments but, among all the possible orientations of these alignments, only one will appear. The interplay between molecular interactions and fluctuations due to molecular noise will draw the system to “choose” among the several possible orientations. In other words, if one state becomes unstable and if new equivalent stable states exist then the fact that the system will “choose” is certain but the choice between these new states will be unpredictable since each state will be evenly likely to emerge. Likewise, when several food sources of identical quality are concurrently available in the nest surroundings, mass-recruiting ant species will be highly sensitive to even small random fluctuations in interactions between nestmates. Any slightly unbalanced distribution of workers and/or uneven amount of trail marks over the different foraging paths can lead the whole colony to select only one resource. This random component in the symmetry-breaking process implies that the choice of one foraging path or food site is probabilistic and unpredictable.

Stochastic methods such as Monte-Carlo simulations proved to be useful to sort out the main effects arising from such fluctuations inherent to trail recruitment. For instance, in a Y-shaped setup where ants have to choose between two foraging paths, random aspects can be automatically incorporated in the different steps of the simulated recruitment. Firstly, the coming or not of an ant to the choice point occurs at random. Secondly, the choice of the trail is a probabilistic one, the probability for each newly coming ant to follow one trail (see Eq. (1)) being updated at each simulation step according to the relative amount of pheromone actually laid on it. Fluctuations in the number of foragers exiting the nest and/or choosing one trail ultimately lead, through amplification processes, to the selection of only one food source in a binary choice.

In the case where ants have to choose between several competing resources of same quality, the behaviour of the system become more complex and show different stable states depending on the number of food sources [36, 96] (Fig. 4). For a given value of foraging intensity (F), when a small number (S) of food sources is available, foragers focus on one food source only, the others being less and evenly exploited. For a large number of resources, the system tends towards a homogeneous state in which all food sources are equally exploited. For intermediate numbers of sources, depending on fluctuations, the colonies will randomly adopt either an equal foraging on multiple sources or a selective exploitation on a single resource. This confirms that quite different patterns can emerge out of the same experimental conditions provided that fluctuations coupled with amplifying mechanisms occur in non-linear systems. While this observation is familiar to physicists, it casts new light on the origin of patterns' diversity in insect societies which is often assumed to find its roots in a corresponding variety of individual behaviour. However, the above examples show that a diversity of patterns may also outcome from the sensitivity of ant societies to fluctuations, independently of any qualitative changes in the behaviour of the individuals.

3.4. *Population size matters*

The emergence of self-organized patterns is intimately related to the existence of critical density of interacting units. For instance, reactions which are well-known for generating oscillations or spatial patterns (e.g. Belousov–Zabotinsky reactions) never display such structured patterns at low concentrations of reactants [49].

Since ant collective patterns emerge out of the multiple interactions between nestmates, they strongly depend on colony size in a non-linear and discontinuous way. A main effect of increasing group size is the higher potential for

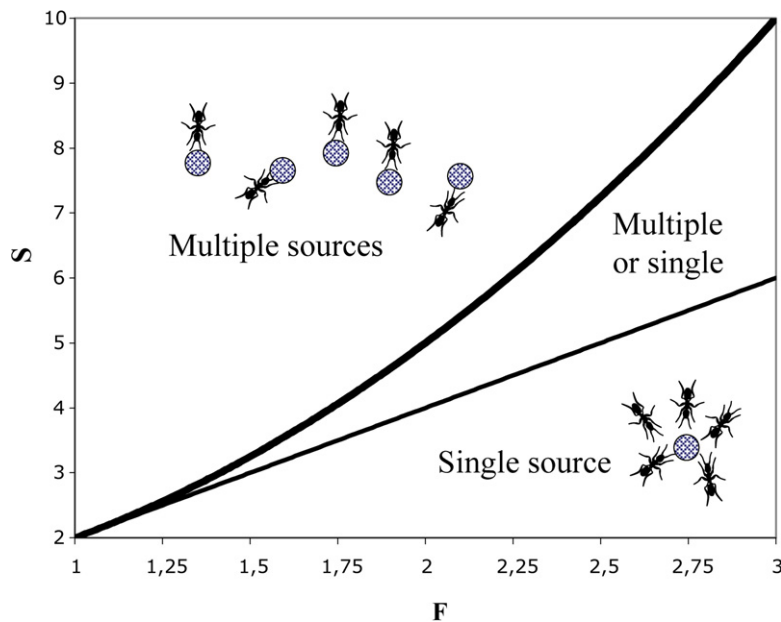


Fig. 4. Pattern of exploitation of food sources as a function of the number of sources (S) and the foraging intensity (F). F values stand for the combined effects of colony size (foragers' flows), trail-laying intensity and trail lifetime (for further explanation see [95]).

amplification processes and related outcomes. For instance, large colonies with a high number of interacting individuals more often bifurcate and adopt a pattern where one area is preferentially foraged whereas small colonies scatter the ants without concentrating their whole worker force on one site. Furthermore, colony size influences foraging choices when faced with multiple food resources (Fig. 4). Small group sizes (small F values) vary considerably in the spatial distribution of foragers since they can either evenly exploit food sources or concentrate their activity on a subset of resources. This variation falls quite rapidly in large colonies which select one source earlier and in nearly all cases [36]. From a functional perspective, it seems optimal for large colonies to concentrate their effort on a limited number of resources so that the number of cooperating nestmates will be as high as to ensure their monopolization by the colony. By contrast, small colonies of which nestmates are too few to defend resources will rather follow an opportunistic strategy: they will intensify their search for food by scattering workers over the foraging range, will exploit concurrently a large number of resources and will readily abandon them when faced with competing species. A large colony size also favours phase transition between disordered and ordered collective behaviour. For example, small colonies of the pharaoh ant (*Monomorium pharaonis*) forage in a disorganized manner (no trail) with a transition to organized pheromone-based foraging in larger colonies. This lack of transition in small colonies is presumably due to the volatility of trail pheromone of which the amounts are too low to nucleate an ordered foraging [9]. Similar effects of colony size may operate for many other collective activities such as nest building [22], brood rearing [22] or exploration of new areas [42]. Indeed, with increasing colony size, exploratory patterns range from a random exploration (or a “disordered” pattern) towards a directed motion over exploratory trails (Fig. 5). The difficulty of small-sized societies to nucleate exploratory trails is not the result of any quantitative difference in the trail-laying behaviour of the individuals. Instead, it is a direct consequence of the small number of participants which cannot reach the critical amounts of trail pheromone needed to nucleate a well-defined trail.

Colony size is thus an attribute of major importance for the good implementation of amplifying processes and hence for the patterns that will emerge at the colony level. Comparative studies of several ant species find out a correlation between the size of mature colonies and the occurrence of amplifying communication such as trail recruitment [3, 8,9]. Likewise, the relative proportion of trail-laying ants steeply increases as small incipient nests of one species grow to large older colonies [84]. In most of these examples, the existence of a huge number of interacting agents appears as highly correlated with a self-organized collective foraging and with the increased selection of foraging sites. As previously mentioned, such focusing of foragers at one location favours cooperation-based activities (e.g as food defense or collective food retrieval) which are expected to be more efficient in large colonies.

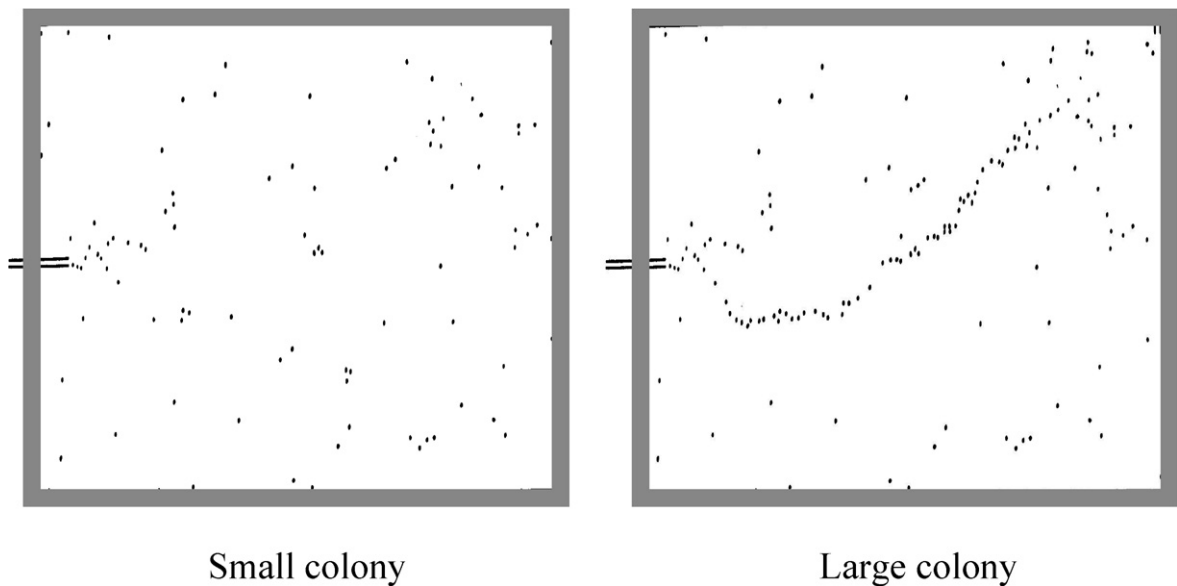


Fig. 5. Pattern of exploration in small-sized (500 ants) or large-sized (1000 ants) colonies. Dots represent the spatial location of *Pheidole pallidula* ants on the experimental area after two hours of exploration, the double line stands for the nest entrance. Based on Detrain et al. [42] data.

3.5. Sensitivity to environmental features

The environment may shape emergent structures in physico-chemical systems by inducing small changes in the interactions between their units. For instance, heating which alters the strength of molecular links will, at a critical temperature, induce a transition from a solid to a liquid phase and, within the liquid phase will lead to a diversity of Bénard convection patterns. Likewise, any environmental factor that alters—even slightly—interactions between nestmates will shape the dynamics of food exploitation and the foraging structures to appear. The environment may act through different but non-exclusive ways: it can either directly influence the behaviour of the individuals or the properties of the information-laden signals that release ants' behaviours.

A first impact of the environment is to induce changes in the behaviour of individual ants and/or in their rate of interactions. For instance, the ambient temperature [125] which influences the activity level or the running speed of foragers determines the flow rates of trail-laying ants and then acts upon the gathering of ants into a foraging column. Likewise, an environmental factor that alters ants' movement or perception range can deeply influence the patterns that will emerge at the collective level [27,47,48]. For instance, in army ant species, the traffic over trails is organized along unidirectional lanes because of two minor elements of locomotion; the angle of the perceptual zone ahead of the ant which influences the distance at which a nestmate will be detected and the avoidance turning rate which determines the extent to which each ant turned away from each other in an encounter. If environmental conditions (e.g. vegetation density, physical heterogeneities) make those parameters fall outside a narrow range, collective orientation and unidirectional flow will not emerge [27]. The biotic environment (e.g. the distribution of food resources, the presence of predators/competitors, ...) can also determine the spatial pattern of foraging. For example, although predatory raids of army ants exhibit the same basic structure, they differ between-species in the number and the dichotomy level of trails simply due to differences in the spatial distributions of exploited food items [Fig. 6, [33,53]]. *Eciton hamatum* species which forages over a few long trails, feeds on scarce but large resources (e.g. social insect nests) whereas *E.burchelli* species with its numerous branched trails, feeds on small arthropods which are easily found but in small densities. Experimental manipulations of prey distribution confirm that a shift from a homogeneous prey distribution to a few large clumps of food items makes the front of the *E.burchelli* raids splitting into a few well-defined trails and sub-swarms [53]. Likewise, numerical simulations predict that a simple increase in the number of food sources prevents the focussing of colony activity on a few trails and favours an equal exploitation of all sources in a more diffuse pattern [Fig. 4, [95]].

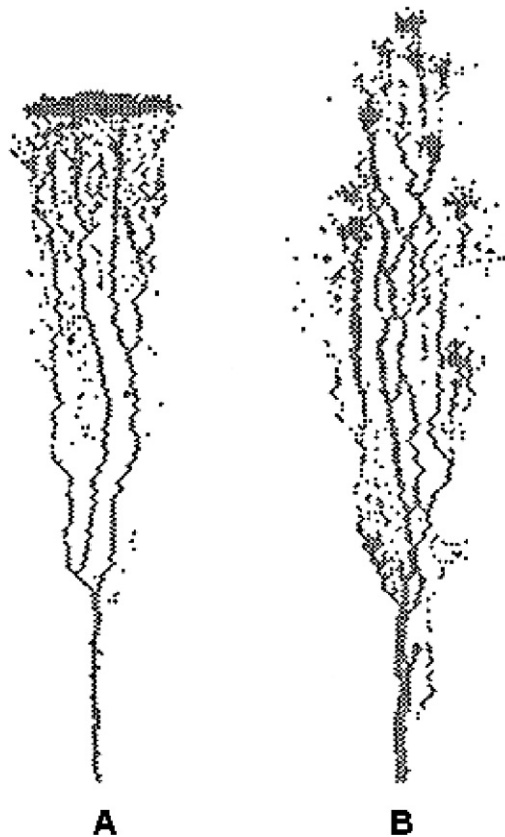


Fig. 6. Distinct foraging patterns in army ants. Results from Monte Carlo simulations based on the same model with two different food distributions. (A) each point has a 0.5 probability of containing 1 food item; (B) each point has a probability of containing 400 food items. In the model simulation, ten ants per step enter the foraging area and, if they find food, they return to the nest laying 1 trail pheromone unit. At each point, the probability of moving per time step increases with the total quantity of pheromone ahead left and right. The probability of choosing between left and right is given by Eq. (1) (see text, for a complete description, see [33]).

A structuring role of the environment can be extended to other communal activities. For instance, the structure of ant nests may be partially driven by the environment such as soil physical properties (e.g. weight of particles) which may influence the digging dynamics of individual workers and guide the development of new galleries in the most favourable zones [31]. Structures like advancing swarms of army ants or extending nest galleries are thus dynamic processes which “evolve” as the ants interact with their environment and which lead to final patterns that one cannot anticipate from the simple observation of the individual behaviours.

A second, far less known, way for the environment to shape collective structures is by altering the communication itself. Depending on its physico-chemical properties, the environment influences the propagation as well as the lifetime of a signal and hence determines the dynamics of interactions between nestmates while keeping unchanged the behaviour of the individuals. For instance, the substrate absorbency alters the accessibility of the trail pheromone to foragers [11,44,75] and may orient the collective choice of one path as well as the preferential foraging over a given substrate. Such sensitivity of self-organized structures to abiotic conditions may apply to other information-laden signals such as vibrations produced by stridulating ants [6] or drumming signals produced by workers inside their nests [55] where the amplitude of the signal and its recruitment range depend on the physical properties of the substrate.

Looking at ants’ collective patterns as self-organized systems has underlined the role of the environment. Instead of acting simply as a constraint on ants’ behaviour, the environment and its properties now appear as actors in the pattern formation process.

In the first part of this review, we show that self-organization provides interesting answers to a question essential to any field of behavioural sciences: how individuals which may at first behave independently and show a slight preference for one or another environmental condition will suddenly behave in a coordinated way and will

make an unanimous choice. We have explored the striking analogies existing between SO patterns occurring in physico-chemical and social systems. Their units interact following similar logics, even though these interactions are implemented in quite different ways (i.e. a trail-following behaviour has no direct equivalent in physico-chemical systems). Furthermore, the prevailing role of amplification processes makes them share common properties such as a strong dependence on the number of interacting units or a high sensitivity of the whole system to fluctuations and environmental changes. These properties of SO systems find a specific echo in the field of behavioural sciences as an answer to the surprising emergence of qualitatively different collective behaviour as one simply gradually tune a few parameters at the individual level. A diversity of collective structures may arise simply by changing some of the initial conditions (e.g. the resource distribution) as well as the amplifying properties of positive feed-backs (e.g. the evaporation rate of the trail). In living organisms, there is a second basic type of tunable parameters: those that are intrinsic to the organism itself. The next part of this review will explore this question on how changes in the biological attributes (genetic, physiological or behavioural ones) of the organism itself may result in important changes in the collective behaviour shown by ant societies. In particular, we will see how individuals can actively tune their behaviour as well as their interactions with nestmates depending on the environmental and social context. We will also emphasize on the functional value of SO social patterns as well as on the role of natural selection in the moulding of interaction rules between individuals.

4. Part two: why ant societies cannot be reduced to physicochemical systems?

One may feel a sense of deep connection between physical systems and biological ones when, for example, similar striped patterns are observed both in sand dunes and on animal coats. Although living patterns are often governed by similar processes as the inanimate world, self-organization should always be seen under the light of evolution when applied to biological fields. Indeed, it is undeniable that SO social systems differ from non-biological ones in two fundamental ways.

Firstly, social patterns are not all of equal value depending on their function and on related benefits for one species fitness. Within a set of patterns, natural selection tends to favour any biological trait or mechanism responsible for the emergence of adaptive collective behaviour. This opens to the idea of a “functional SO” meaning that, at the lower level, individual behavioural rules should be selected depending on their ability to produce at the upper level the best adapted collective response [20,24]. In the context of foraging, there will be a selection of the behavioural rules, physiological attributes or physico-chemical properties of amplifying signals which optimize the exploitation of resources, improve the speed and/or accuracy of information transfer or help making an efficient collective decision.

Secondly, there is a higher diversity of types of interactions between units of social systems. The formation of a social pattern obeys the laws of physics or chemistry but also includes physiological and behavioural aspects. No ant looks like another and each individual is characterized by a specific behavioural profile. Although it would be out of reach and out of scope of the present review to cover all the aspects that govern social differentiation in ants, one may say that the genetic background, the caste belonging, the sensory integration or the own experience of each worker determine its likelihood to interact with nestmates, to react to environmental cues or to respond to signals emitted by congeners. Ant societies are thus assemblages of interacting individualities and offer an efficient blend mixing individual specificities and collective “unanimity” in the implementation of functional responses.

The aim of the following section will be to demonstrate that “ants do not behave like molecules”. With its 10^6 neurons and numerous sensors, each ant individual is a sensitive unit which can process a lot of information. This complex creature follows decision rules, modulates its interactions with nestmates, tunes emitted signals or exhibits variations in its response thresholds in order to cope with complex and changing situations. As a result, ants do not passively undergo the structuring effect of self-organizing mechanisms but instead, play a proactive role in pattern formation. By “acting upon” some parameters of the system, ant workers can invoke the onset of a structure or of a collective choice.

At first, we will show that ants can tune the level of noise between interacting individuals—meaning the accuracy of information transfer between an emitter and a receiver. We will examine from a functional perspective, how such individual tuning of noise influences the global dynamics of transition from one pattern to another.

Secondly, we will review the mechanisms through which the ant individuals assess the opportunities/constraints of their environment, tune their interactions with nestmates and hence orient choices made by the whole colony. We will

emphasise the use by ants of intelligent decision criteria which incidentally integrate a variety of environmental and social parameters.

4.1. Ants tune system noise

Noise is an intrinsic component of any dynamic system. In the case of ant species using mass communication by chemical trails, “noise” between interacting units takes the form of incidental loss of trail paths by recruited ants. Indeed, through the combined effects of molecular diffusion, air turbulence and/or local heterogeneities in the trail amount laid by scouts, ants have to orient into an odorant channel of which pheromone concentrations fluctuate at both large and small length scales. This makes an accurate trail-following difficult to achieve especially at the beginning of recruitment. Moreover, recruited ants that attempt to reach the discovered food sources walk in a cosine way and may subsequently exit the active space of the recruitment trail [19,68]. For a given food distance from the nest, the number of “lost” ants can be considered as an estimate of the level of “noise” within the system. While noise is usually seen as an unwanted draw-back in human activities, it has a twofold—positive and negative—effect on the fitness of insect colonies. On the one hand, the loss of the trail by foragers obviously decreases the number of individuals reaching the target and then the food retrieval efficiency. On the other hand, “lost” individuals may be beneficial to their colony: they prevent it from falling into static configurations where some locations receive disproportionate attention while others remain unexploited. Since each exploring individual cannot directly compare all available resources, “lost” ants help to find optimal solutions at the colony level as schematized in Fig. 7. The random walk of foragers gives rise to a

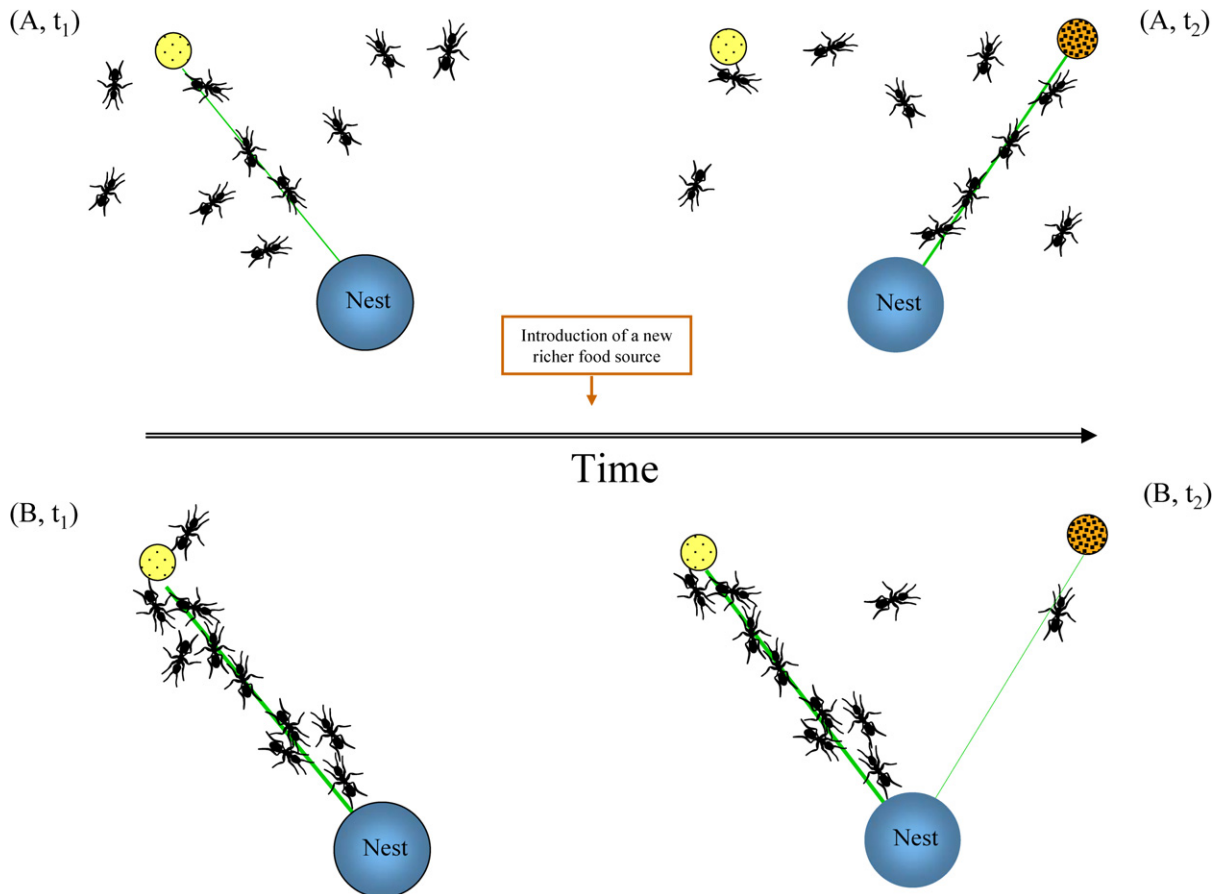


Fig. 7. Noise influences the flexibility of foraging. (A) For a high level of noise (poor individual trail-following), ants are scattered around the foraging trail (t_1) and, if a richer food (orange) is introduced later on (t_2), they are likely to discover this new source and to exploit it preferentially. (B) For a low level of noise (accurate individual trail-following), all ants are focused over the first trail (t_1) and when a new richer source is introduced (t_2) most of foragers will remain “trapped” in the first suboptimal exploitation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bell-shaped distribution of workers centred on the main trail, this distribution being wider when a diffuse exploration and a high level of noise occur (Fig. 7; A, t_1). Those ants which get lost over the food path wander around for a period of time and are likely to find out a new and possibly richer resource. The newly discovered rich source will then draw most of the foragers (Fig. 7; A, t_2). By contrast, when the trail is too accurately followed by workers, very few ants will get lost (Fig. 6; B, t_1) what makes unlikely the discovery of new resources (Fig. 7; B, t_2). A counterintuitive property of noise in social systems is thus to be a component of collective decision-making [37]. Not only do structures emerge despite noise but fluctuations become essential to pattern formation. They act as seeds from which collective decisions emerge and new solutions are discovered what prevents the colony being “trapped” in suboptimal patterns.

The ability for an ant species to control the level of noise appears as a major evolutionary gain since it allows to achieve, at the colony level, the proper balance between noise leading to innovations—i.e. new food discoveries—and efficiency of communication. A simple way for ants to tune communication accuracy is by modifying the intensity of information-bearing signals (i.e. the trail amount laid over the substrate) emitted by exploring ants—also called scouts. Ideally, the ant colony is expected to maximize the accuracy of trail-following at the expenses of innovating discoveries by lost ants as the quality of exploited resources increases. Actually, ant scouts are more prone to lay a recruitment trail as they return from a richer food source (e.g. a droplet of high sucrose concentration) [133], for a review see [43,72]. By doing so, scouts help recruits to climb the pheromone gradient, reduce the percentage of lost recruits and ultimately they facilitate cooperation in the exploitation and the defense of the best available food resources [100] or nesting sites [73,74].

By tuning the signal/noise ratio, scouts also determine the spatial distribution of ants between foraging sectors. Due to the snowball effect of trail communication, symmetry breakings in which foragers’ activity concentrates into a limited number of sites are more likely to occur for stronger chemical trails. In this respect, a tuning of noise and of motion patterns depending on food nature allows foragers to adjust *in fine* the spatial distribution of the search effort and/or the food exploitation to that of available resources [80,101]. For instance, the nature—proteinaceous or carbohydrates—of food governs the recruitment decision of scouts and leads to a quite different spatial allocation of foragers. A strong recruitment is launched and a marked choice of one (or a few) sources is observed to carbohydrates that are rich and long lasting sources of honeydew. Conversely, a weak trail-laying to proteinaceous sources leads to an even distribution of foragers that maximizes the discovery and intake of new preys which are often scattered food items [101].

Finally, one should cite other means by which ant societies can exert a control on the system noise. For instance, if the ants first discover and establish a trail to a low energy source, the recruitment to this poor source may be too strong for more profitable sources to compete even though individual foragers increase their trail-laying intensity [100,117, 126]. Some ant species which perform group recruitment [71,72,129] tackle this problem and limit the occurrence of sub-optimal situations. Indeed, experienced individuals directly guide groups of recruits to the discovery site and are able to reorient the choice towards the exploitation of richer resources while foragers of mass-recruiting species will not. As a rule, such increased reliance on a few well-informed leader ants may slow down the recruitment growth but, on the other hand, limits the hazardous issues of fluctuations especially at the beginning of recruitment and allows overcoming constraints set by a number of workers misforaging on a poor source.

There is an additional and even more subtle way for ants to reduce noise while foraging: this is achieved at the individual level through the internal process of learning. Unlike molecules, the behaviour of ant individuals (e.g. their response threshold to stimuli) change as time goes on depending on their personal experience. Namely, ants are capable of associative learning by linking food rewards to previously meaningless stimuli such as visual landmarks or topochemical stimuli [69,72]. Furthermore, social learning can be achieved by tandem running ant species, in the sense that an experienced leader can “teach” to a naïve pupil worker how to reach a target such as a new food source or a new nesting site [54] see also [79]. There is a bidirectional feedback loop between tandem running ants: when antennal contact between the pair is lost, the leader slows down and the follower accelerates to catch up [90]. This intimate interaction minimizes the system noise and the number of “lost” recruited ants while allowing the follower to memorise the path as well as related landmarks. Learning, either individual or social, improves foragers’ orientation and thereby reduces the impact of noise on communication and pattern formation. By doing so, memory favours fidelity to rewarding sites and, at the colony level, maintains activity on these sites over long time scale.

Throughout the evolution, ants have thus developed several behavioural means which enable them to tune their interactions with nestmates as well as the dynamics of information transfer. At the colony level, patterns are formed

which are the best compromise between maximizing the accuracy/efficiency of food exploitation and keeping some level of noise leading to new discoveries.

4.2. Simple rules and complex decisions: the use of “intelligent” criteria

Beyond being simply an ordered arrangement of workers, an ant collective pattern can be seen as an information network out of which a communal decision arises. In non-linear systems like ant societies, a wide variety of collective patterns can be generated by a surprisingly small set of interaction rules which involve information transfer between individuals (see e.g. [20,43,116]). In natural conditions, the information that can be potentially shared among interacting nestmates is highly diverse, complex and unlimited. In this respect, exploring scouts which are the best-informed workers are the primary agents who will decide to transmit information to nestmates and who will launch food recruitment by the laying of a chemical trail. Since it is obviously impossible for each ant to get an exhaustive picture of their environment in a reasonable amount of time, scouts have to rely on a few functional criteria based upon the local information they acquire moment by moment. These criteria govern behavioural rules of thumb which can be presented in the form of a brief “if-then” statement such as “if I cannot retrieve alone this food item, then I lay a recruitment trail”. These rules may be simple in their logic but, ultimately, they produce efficient group-level response such as the choice of the best resource, the avoidance of risky areas and so on.

While shifting towards another state has no consequence on a system made of interacting particles, the success or failure in bifurcating towards the exploitation of the best resources has an impact on population growth and reproductive success of ant societies. In particular, recruitment decision rules should be based on straightforward, functional and highly relevant criteria [41,107]. For instance, a simple decision rule can be to increase the amount of recruitment pheromone laid over trails as a function of food quality such as the sugar concentration of honeydew. In a binary choice between two food sources of different quality (see Eq. (1)), the amount of pheromone (x) on the branch leading to a rich food source will be higher and hence this branch more likely to be followed. This allows an efficient adjustment of colony investment to the energetic value of available resources (see e.g. [7,15,133]). More generally, one way for insect societies to reduce penalties for incorrect collective decision and to cope with the complexity of their environment is the use of decision rules based on “intelligent” criteria. For example, when scavenging for preys, a simple recruitment criterion accounts for the variety of *Pheidole pallidula* foraging patterns which show all stages intermediate between an individual retrieval of small items to mass exploitation of large preys by a foraging trail (Fig. 8).

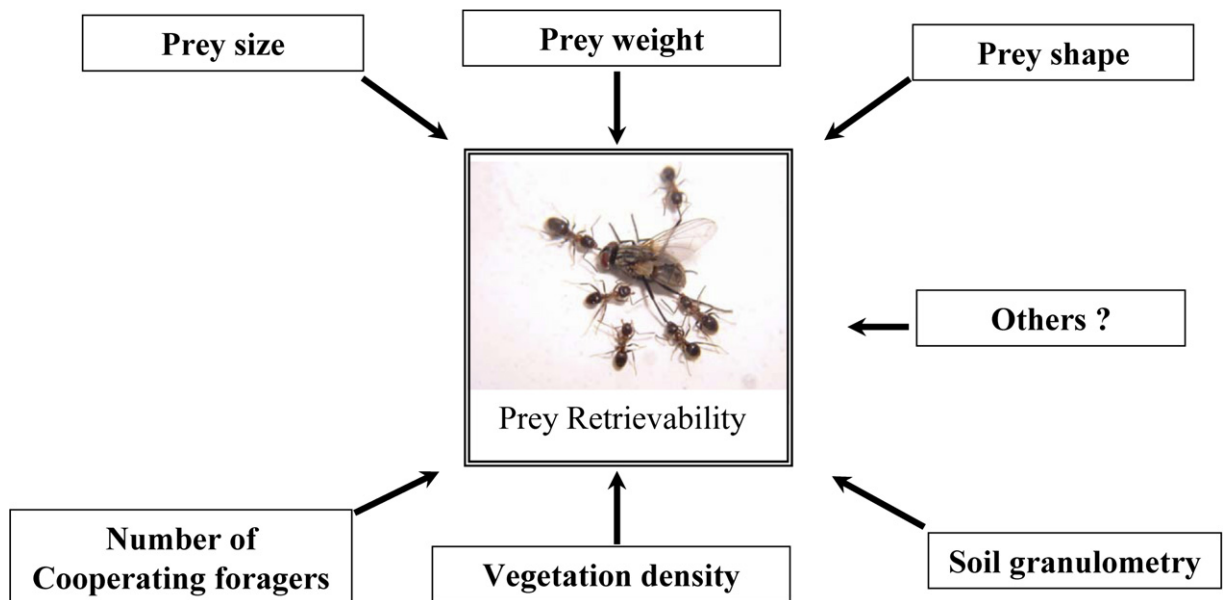


Fig. 8. Example of an intelligent criterion. The ability of one individual to retrieve the prey determines its recruitment decision and hence collective foraging patterns. Several parameters are incidentally integrated on the “Prey retrievability” intelligent criterion. Photograph of cooperative prey exploitation by *Lasius emarginatus*. ©A. Nivaggioli.

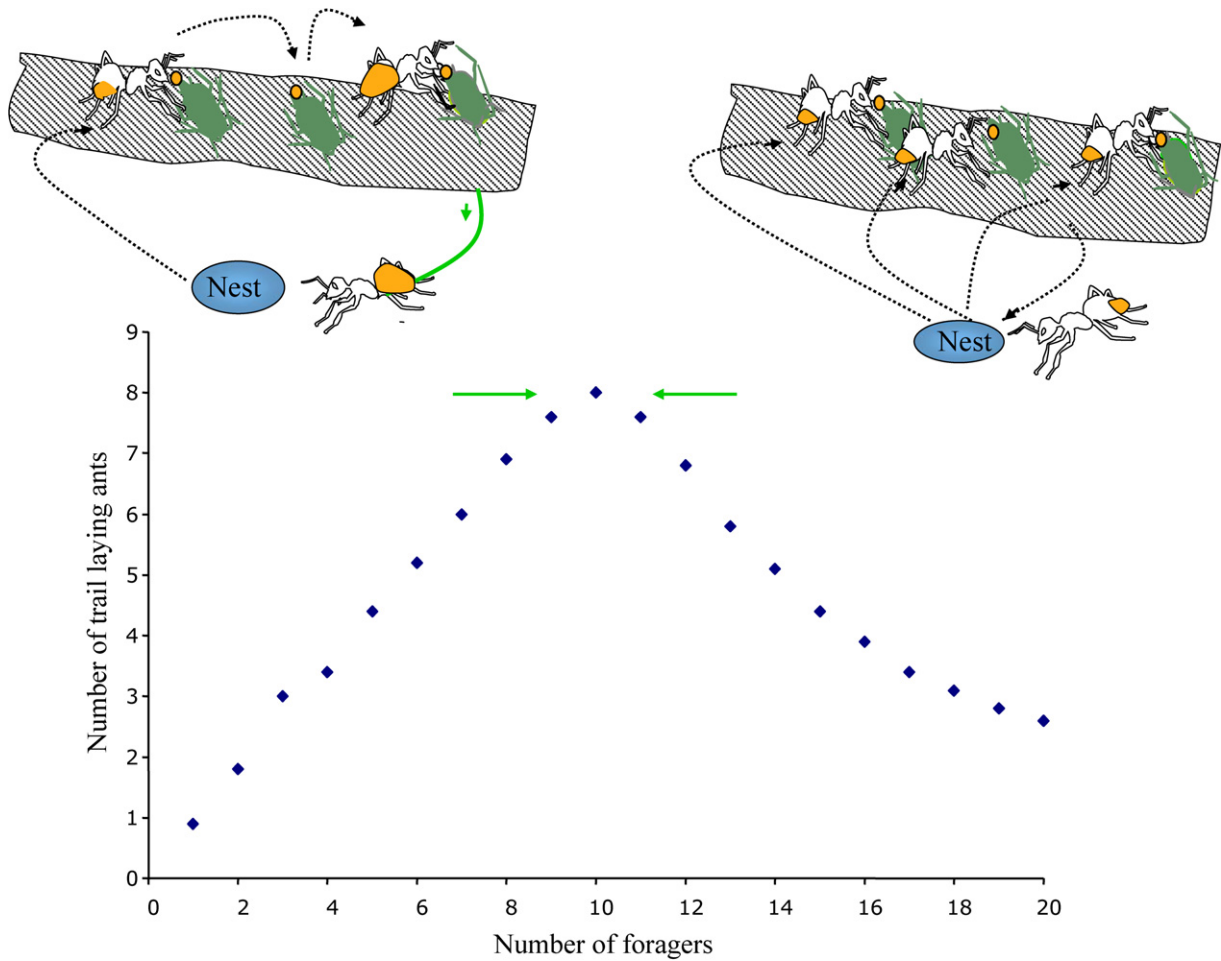


Fig. 9. Regulation of ants' foraging to resources' productivity. For a given amount of honeydew, there is a number of foragers at which recruitment intensity (N trail-laying ants) is maximal. Below this maximum value (left side drawing), each ant can fill in its gaster and will lay a trail when returning to the nest. Above this maximum value (right side drawing), several foragers concurrently exploit aphids being unable to reach their desired volume. All of them will then return to the nest without laying a trail.

This criterion is the prey retrievability: a scout decides to recruit nestmates as soon as it cannot individually retrieve the prey [40]. A very large prey then elicits a very intense trail, draws larger number of recruits as well as due to their higher response thresholds to the trail pheromone, large-headed major workers specialized in the cutting of prey [45]. The “prey retrievability” criterion is a seemingly crude estimator of prey size but it is highly functional since it automatically integrates information about the size, the shape and the weight of the prey but also about environmental factors that may influence food transport (e.g. the vegetation density or social factors like the number of cooperating ants) (Fig. 8).

In the case of liquid food sources, another “intelligent” decision criterion is used by scouts that is “the ability to ingest a desired volume” [83]. This means that before deciding to recruit nestmates, each forager has to find out enough food as to ingest a desired volume of its own. Though very simple, this recruitment rule based on an individual threshold enables a colony to adjust the number of tending ants to the honeydew production of aphids [85]. For a given honeydew amount, there will be a number of foragers that maximises recruitment (i.e. the number of trail-laying individuals). This optimum is reached as follows (Fig. 9). At the beginning of food exploitation, all the foragers having found out the food source can ingest their desired volume and go back to the nest laying a trail. This increase in the number of foragers will progressively slow down as the food source is becoming exploited by larger number of foragers. At this time, competition between feeding foragers will increase around aphids making more difficult the reaching of their desired volume and then decreasing the fraction of trail-laying individuals among

returning ants. This reduced trail-laying intensity will lower the number of exiting foragers and will draw back the system towards the maximum. The “desired volume” rule of thumb thus automatically slows down recruitment to overexploited food sources and self-regulates foragers’ recruitment to the size of resources. The “desired volume” is also a highly integrative criterion since it incidentally assesses many factors related to honeydew production such as the number of aphids, the size and renewal rate of emitted droplets but also to ant colony demands such as its nutritive needs or the number of ants already feeding at the food source. In other contexts such as nest emigration [86] or brood rearing [21], one may also find out decision rules based on criteria that, in an ever-changing environment, allow ants to make rapid decisions instead of perfectly informed ones based on multiple time-consuming assessments. Furthermore, by using intelligent criteria relevant to a behavioural strategy, ant species “reduces” the sensory, physiological and behaviour capabilities that need to be genetically coded in the individuals.

4.3. *Ants estimate the number of conspecifics*

In physico-chemical systems, the laws of interaction between units are invariant whatever the number of interacting particles. The situation is quite different for ant societies: each worker may tune its behaviour as well as its interaction pattern depending on its perception of the number of nestmates which are present either locally or within the whole colony [84,123]. For instance, in *Lasius niger* ant species, one can find out such a “sense of number” by the individuals. Indeed, scouts will more likely launch trail recruitment and a collective food exploitation when living in large colonies containing several hundredths of ants than scouts from small incipient colonies which will essentially perform individual food retrieval. One cannot actually say whether this change is due to a short-term effect of colony size on the releasing of trail-laying behaviour or to a long-term alteration of scout physiological abilities to produce this chemical signal. From a functional perspective, the paucity of trail-laying behaviour in incipient colonies fits the discrete foraging of their few workers patrolling at short distances whereas trail recruitment in large ant colonies supports a strategy of monopolisation and active defence of resources against competitors.

Ants have developed “statistical” tools to assess the occupancy level of a location and to accordingly shape their behaviour and communication. Direct physical contacts with other workers can become devices for individuals to track group size without requiring them to count. Indeed, there is a basic spatial relation between group size and interaction patterns: if some ants walk around randomly, the number of times they will bump into each other and the time elapsed between encounters will depend on ants’ density [62]. Some ant species could use the rate at which they contact others as an indication of nestmates’ number in order to accordingly tune their way of behaving [60,62] but see [97]. In harvester ants, this social cue governs division of labour within the colony since the individual decision to switch from one task to another depends on its recent history of interactions with workers already performing this task [61]. Likewise, in the context of nest emigration, rates of physical contacts allow *Temnothorax* scouts to assess whether a quorum number of nestmates is reached and whether recruitment should be launched toward a new nesting site [102]. The ability of individuals to assess the number of conspecifics is also at the core of territorial strategies by eliciting changes in aggressive responses [16,82,108]. For instance, in *Myrmecocystus* honeypot ants, mass confrontations with conspecific competitors take the form of tournaments of fighting displays. When two hostile workers meet, they bend the gaster toward the opponent, drum intensively the other with their antennae and kick it with their legs. After a while, one usually yields and the winner soon meets another opponent before returning to the nest and recruiting tenths of workers to the fighting area. The recruitment decision of these scouts is determined by their assessment of one another’s strength during the tournaments. Since each scout is unable to perform “head counting” of all fighters, enemy’s strength is assessed by the rate of encounters it has experienced but also by the queuing—that is the time spent before meeting an unengaged opponent. A long wait before meeting an enemy means a small colony whereas a short wait means a large dominant colony [82].

In all these examples, ants proved to be able to assess the density of nestmates through the pattern of interactions they have experienced. Nonetheless, physical encounters with congeners are not always required since any indirect cue related to the presence of workers can become an estimator of ants’ density. For instance, the concentration of foot print marks which, unlike the trail pheromone, are passively laid by ants during their exploration of nest surrounding, provides such a social cue: the higher the occupancy of a location, the higher the amount of home-range marks left over the substrate. Experiments show that home-range marks influence the tendency of ants to rest at a given location [39] or to lay a recruitment trail [46]. Indeed, the emission of the recruitment trail is triggered by the likelihood that this signal will be perceived by receivers. Integrating the use of a density cue in the decision-making process

of scouts is highly adaptive for mass-recruiting species of which foraging success is closely related to the number of foragers which are locally present and available for cooperation, especially when large and/or renewable food sources are discovered. Besides, a decreased trail-laying towards weakly explored areas will reduce the number of ants mobilized to less frequented areas that are potentially risky and dangerous. One may expect that the use of such social density cues is widespread and applies to other non-foraging activities. For example, simulations show that patterns of respiratory products (CO₂ levels) which are directly related to workers' density and activity—may shape collective patterns of aggregation within the nest [29].

Ant individuals are thus sensitive not only to environmental constraints/opportunities but also to the social context in which they live. They shape their behaviour depending on social estimators which can be direct cues like encounter patterns or indirect cues produced by the insect themselves such as patterns of chemical marks on the floor or gradients of respiratory gases. A tuning of communication based on such social cues has a great potential for efficient dynamic results since there is a direct feed-back between the actual presence of insect workers and the pattern being expressed at the collective level.

5. Conclusion

Physico-chemical patterns are phenomena without any adaptive significance: there is no selective force that pushes the development of sand ripples or of spiral waves in chemical reactions. By contrast, biological patterns are selected throughout the evolution as far as they improve the survival and reproductive success of one species. Like the tiger stripes facilitate its camouflage within vegetation, a functional adaptive value can be associated to social patterns. Ideally, insect societies are expected to display the collective pattern that maximizes the average benefit of nestmates for a given set of environmental conditions whereas any depart from the optimal strategy would be condemned. Many evolutionary theories—optimality theory, game theory, population genetics were built on models describing why a behavioural pattern is ultimately displayed by an animal group [57,87]. Such theories have been the foundations of behavioural ecology for many years but often make assumptions without a knowledge of the involved mechanisms. As regards social patterns, there is now a need for additional perspectives focusing on the dynamics of emergence as well as on the regulatory processes that produce them. In other word, no evolutionary stance about collective structures is fully plausible without a careful examination of the underlying rules since they constrain the range of possible strategies emerging at the colony level.

This review shows that self-organisation is a powerful set of pattern-generating mechanisms or, in other words, is a powerful generator of biological diversity. As such, natural selection has taken advantage of these mechanisms to solve a variety of problems faced by many group-living organisms including bacteria colonies [10,112], gregarious arthropods [2,50,73,74], fish schools [28,99] and herding mammals [26,56]. Although the biological and social attributes deeply differ from one of these species to another, similar behaviour rules, coupled with self-organizing processes seem to have been selected as robust and well-adapted means for efficient collective problem-solving [26,116]. Self-organization provides an answer to a challenge of evolutionary biology: how can we generate a wide variety of social patterns in group-living animals while keeping limited the number of behavioural rules and physiological attributes that should be “coded” in the individuals. In this respect, a key property of SO is undeniably its ability to generate new patterns by making only small adjustments of the system parameters and by keeping a remarkable economy of behavioural rules at the individual level. Such economy is achieved through different and complementary ways.

At first, the basic ingredients of SO—positive feed-backs and amplification of fluctuations—give birth to different group structures out of identical environmental conditions. Like in physico-chemical systems, several possible states of the system exist (multistationarity) and discrete qualitative changes may emerge as one parameter gradually varies (bifurcation). In particular, even slight differences in the emission or response threshold of individuals to signals induce large changes in the group properties and trigger quite different colony-specific structures. One may assume that, throughout the evolution, the tuning of a behavioural parameter is enabled for a range of values close to a bifurcation point, thereby endowing the group with the ability to switch from one behavioural response to another. Tunable parameters and bifurcation thus provide self-organized societies with a unique efficient mechanism for producing flexibility and adaptiveness. Such flexibility may operate on a day to day basis, over a longer seasonal time span or even between species at an evolutionary time scale.

A second source of economy relies in the limitation of decision rules (e.g. the decision to lay a trail) to a few but highly functional ones. The use of “intelligent” decision criteria allows the animals—including solitary ones—to

incidentally integrate multiple factors which would otherwise require a specific detection and decoding of sensory inputs. These simple decision rules coupled with amplifying processes appears as easy ways for insect societies to solve a variety of problems.

At last economy is provided by environmental parameters which may act not only as constraints but also as tuners of self-organized behaviour. Keeping the same set of behavioural rules, the environment may alter patterns of interaction between nestmates as well as the dynamics of information transfer and thereby may determine the emergence of collective structures.

When combined, these three types of complexity-generating mechanisms lead to an exploding number of patterns that can be potentially displayed by the colony. This sheds some light over one of the mysteries of biology: how the enormous behavioural complexity of group patterns can be achieved without requiring the same level of complexity of the behavioural algorithms or on what needs to be genetically coded in the individuals.

As regards the future of this approach, while self-organization is a familiar term in the fields of chemistry, physics, much is still needed to achieve acceptance and to recognize the utility of the “self-organization concept” in the biology of organisms. A current weakness is certainly the paucity of experiments in which self-organizing mechanisms have been clearly identified. To fill this gap, we need to develop modelling and experimental procedures which are specifically designed to distinguish between hypotheses about pattern formation. This makes the study of social insects’ organization particularly exciting as a first proof that complexity sciences and sociobiology can mutually benefit from a cross-fertilization.

Acknowledgements

We would like to thank Luc Dekelver for his help in editing the manuscript as well as all members of our research unit for fruitful discussions. C. Detrain and J.L. Deneubourg are senior research associates of the Belgian National Fund for Scientific Research.

References

- [1] Altshuler E, Ramos O, Nunez Y, Fernandez J, Batista-Leyva AJ, Noda C. Symmetry-breaking in escaping ants. *Am Nat* 2005;166(6):643–9.
- [2] Ame JM, Halloy J, Rivault C, Detrain C, Deneubourg JL. Collegial decision making based on social amplification leads to optimal group formation. *Proc Nat Acad Sci* 2006;103:5835–40.
- [3] Anderson C, McShea DW. Individual versus social complexity with particular reference to ant colonies. *Biol Rev* 2001;76:211–37.
- [4] Bak P. *How nature works?* New York: Springer; 1996.
- [5] Ball P. *The self-made tapestry. Pattern formation in nature.* Oxford: Oxford University Press; 1999.
- [6] Baroni-Urbani C, Buser MW, Schillinger E. Substrate vibration during recruitment in ant social organization. *Insectes Sociaux* 1988;35:241–50.
- [7] Beckers R, Deneubourg JL, Goss S. Modulation of trail-laying in the ant *Lasius niger* and its role in the collective selection of a food source. *J Insect Behav* 1993;6:751–9.
- [8] Beckers R, Goss S, Deneubourg JL, Pasteels JM. Colony size, communication and ant foraging strategy. *Psyche* 1989;96:239–56.
- [9] Beekman M, Sumpter DJ, Ratnieks FL. A phase transition between disordered and ordered foraging in Pharaoh’s ants. *Proc Nat Acad Sci* 2001;98:9703–6.
- [10] Ben Jacob E, Becker I, Shapira Y, Levin H. Bacterial linguistic communication and social intelligence. *TREE* 2004;12:365–72.
- [11] Beugnon G, Dejean A. Adaptive properties of the chemical trail system of the African weaver ant *Oecophylla longinoda* Latreille (Hymenoptera, Formicidae, Formicinae). *Ins Soc* 1992;39:341–6.
- [12] Boi S, Couzin ID, Del Buono N, Franks N, Britton NF. Coupled oscillators and activity waves in ant colonies. *Proc Roy Soc London B* 1999;266:371–8.
- [13] Bonabeau E, Dorigo M, Theraulaz G. *Swarm intelligence: from natural to artificial systems.* Oxford: Oxford University Press; 1999.
- [14] Bonabeau E, Theraulaz G, Deneubourg JL, Aron S, Camazine S. Self-organization in social insects. *TREE* 1997;12:188–93.
- [15] Breed MD, Fewel JH, Moore AJ, Willimas KR. Graded recruitment in a ponerine ant. *Behav Ecol Sociobiol* 1987;20:407–11.
- [16] Brown MJF, Gordon DM. How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behav Ecol Sociobiol* 2000;47:195–203.
- [17] Buhl J, Deneubourg JL, Grimal A, Theraulaz G. Self-organized digging activity in ant colonies. *Behav Ecol Sociobiol* 2005;58:9–17.
- [18] Buhl J, Gautrais J, Deneubourg JL, Theraulaz G. Nest excavation in ants: group size effects on the size and structure of tunnelling networks. *Naturwissenschaften* 2004;91:602–6.
- [19] Calenbuhr V, Chretien L, Deneubourg JL, Detrain C. A model for osmotropotactic orientation (II). *J Theoret Biology* 1992;158:395–407.
- [20] Camazine S, Deneubourg JL, Franks N, Sneyd, Bonabeau E, Theraulaz G. *Self-organization in biological systems.* Princeton, NJ: Princeton University Press; 2001.

- [21] Cassill DL, Tschinkel WR. Information flow during social feeding in ant societies. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information processing in social insects*. Basel: Birkhäuser; 1999.
- [22] Cassill DL, Tschinkel WR, Vinson SB. Nest complexity, group size and brood rearing in the fire ant *Solenopsis invicta*. *Insectes Sociaux* 2002;9:158–63.
- [23] Cole BJ. Short-term activity cycles in ants: generation of periodicity by worker interaction. *Amer Naturalist* 1991;137:244–59.
- [24] Cole BJ. Evolution of self-organized systems. *Biol Bull* 2002;202:256–61.
- [25] Cole BJ, Trampus I. Activity cycles in ant colonies: worker interactions and decentralized control. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information processing in social insects*. Basel: Birkhäuser; 1999.
- [26] Conradt L, Roper TJ. Consensus decision making in a animal. *Trends in Ecology & Evolution* 2005;20:449–56.
- [27] Couzin ID, Franks NR. Self-organized lane formation and optimized traffic flow in army ants. *Proc Roy Soc Lond* 2002;270:139–46.
- [28] Couzin ID, Krause J. Self-organization and collective behaviour in vertebrates. *Adv Study Behaviour* 2003;32:1–75.
- [29] Cox MD, Blanchard GB. Gaseous template in ant nests. *J Theor Biol* 2000;204:223–38.
- [30] Deneubourg JL, Aron S, Goss S, Pasteels JM. The self-organizing exploratory pattern of the Argentine ant. *J Insect Behav* 1990;3:159–68.
- [31] Deneubourg JL, Franks NR. Collective control without explicit coding: the case of communal nest excavation. *J Insect Behav* 1995;8(4):417–32.
- [32] Deneubourg JL, Goss S. Collective patterns and decision-making. *Ethology, Ecology & Evolution* 1989;1:295–311.
- [33] Deneubourg JL, Goss S, Franks N, Pasteels JM. The blind leading the blind: modeling chemically mediated army ant raid patterns. *J Insect Behavior* 1989;2:719–25.
- [34] Deneubourg JL, Goss S, Franks N, Sendova-Franks A, Detrain C, Chréien L. The dynamics of collective sorting robot-like ants and ant-like robots. In: Meyer JA, Wilson S, editors. *Simulation of adaptive behavior: from animals to animats*. Cambridge, MA: MIT Press; 1991.
- [35] Deneubourg JL, Lioni A, Detrain C. Dynamics of aggregation and emergence of cooperation. *Biol Bull* 2002;202:262–7.
- [36] Deneubourg JL, Nocolis S, Detrain C. Optimality of communication in self-organized social behaviour. In: Hemelrijk C, editor. *Self-organization and evolution in social systems*. Cambridge: Cambridge University Press; 2005.
- [37] Deneubourg JL, Pasteels JM, Verhaeghe JC. Probabilistic behaviour in ants: a strategy of errors? *J Theoret Biol* 1983;105:259–71.
- [38] Depickère S, Fresneau D, Deneubourg J-L. A basis for spatial and social patterns in ant species: dynamics and mechanisms of aggregation. *J Insect Behavior* 2004;17(1):81–97.
- [39] Depickère S, Fresneau D, Detrain C, Deneubourg JL. Marking as a decision factor in the choice of a new resting site in ants. *Insectes Sociaux* 2004;51:243–6.
- [40] Detrain C, Deneubourg JL. Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. *Animal Behaviour* 1997;53:537–47.
- [41] Detrain C, Deneubourg JL. Complexity of environment and parsimony of decision rules in Insect societies. *Biol Bull* 2002;202:268–74.
- [42] Detrain C, Deneubourg JL, Goss S, Quinet Y. The dynamics of collective exploration in the ant *Pheidole pallidula*. *Psyche* 1991;98:21–31.
- [43] Detrain C, Deneubourg JL, Pasteels JM. Decision-making in foraging by social insects. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information Processing in Social Insects*. Basel: Birkhäuser; 1999.
- [44] Detrain C, Natan C, Deneubourg JL. The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften* 2001;88:171–4.
- [45] Detrain C, Pasteels JM. Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant *Pheidole pallidula*. *J Insect Behavior* 1991;4(2):157–77.
- [46] Devigne C, Renon A, Detrain C. Modulation of recruitment according to home range marking in ants. *Animal Behaviour* 2004;67:1023–9.
- [47] Dussoutour A, Deneubourg JL, Fourcassié V. Amplification of individual preferences in a social context: the case of wall-following in ants. *Proc Roy Soc B* 2005;272:705–14.
- [48] Dussoutour A, Fourcassie V, Helbing D, Deneubourg JL. Optimal traffic organization in ants under crowded conditions. *Nature* 2004;428(6978):70–3.
- [49] Epstein IR, Pojman JA. *An introduction to nonlinear chemical dynamics*. Oxford: Oxford University Press; 1998.
- [50] Fitzgerald TD, Peterson SC. Elective recruitment communication by the eastern tent caterpillar (*Malacosoma americanum*). *Animal Behaviour* 1983;31:417–23.
- [51] Franks NR, Bryant S, Griffiths R, Hemerik L. Synchronisation of the behaviour within nests of the ant *Leptothorax acervorum*. I. Discovering the phenomenon and its relation to the level of starvation. *Bull Math Biol* 1990;52:597–612.
- [52] Franks NR, Fletcher CR. Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav Ecol Sociobiol* 1983;12:261–70.
- [53] Franks NR, Gomez N, Goss S, Deneubourg JL. The blind leading the blind in army ant raid patterns: testing a model of self-organization. *J Insect Behav* 1991;4:583–607.
- [54] Franks NR, Richardson T. Teaching in tandem-running ants. *Nature* 2006;439:153.
- [55] Fuchs S. The response to vibrations of the substrate and reactions to the specific drumming in colonies of carpenter ants (Camponotus, Formicidae, Hymenoptera). *Behav Ecol Sociobiol* 1976;1:155–84.
- [56] Gérard JF, Bideau E, Maublanc ML, Loisel P, Marchal C. Herd size in large herbivores: encoded in the individual or emergent? *Biol Bull* 2002;202:275–82.
- [57] Giraldeau LA, Caraco T. *Social foraging theory*. Princeton, NJ: Princeton University Press; 2000.
- [58] Glansdorff P, Prigogine I. *Thermodynamic theory of structure, stability and fluctuations*. London: Wiley; 1971.
- [59] Goldbeter A. *Biochemical oscillations and cellular rhythms*. Cambridge: Cambridge University Press; 1996.
- [60] Gordon DM. The organization of work in social insect colonies. *Nature* 1996;380:121–4.
- [61] Gordon DM, Medhiabadi NJ. Encounter rates and task allocation in harvester ants. *Behav Ecol Sociobiol* 1999;45(5):370–7.

- [62] Gordon DM, Paul RE, Thorpe K. What is the function of encounter patterns in ant colonies? *Anim Behav* 1993;45:1083–100.
- [63] Goss S, Deneubourg JL. Autocatalysis as a source of synchronised rhythmical activity in social insects. *Insectes Sociaux* 1988;35:310–5.
- [64] Goss S, Deneubourg JL. The self-organising clock pattern of *Messor pergandei* (Formicidae, Myrmicinae). *Insectes Sociaux* 1989;36:339–46.
- [65] Gotwald WH. *Army ants: the biology of social predation*. Ithaca, London: Cornell University Press; 1995.
- [66] Halley JD, Burd M. Non-equilibrium dynamics of social groups: insights from foraging Argentine ants. *Ins Soc* 2004;51:226–31.
- [67] Halley JD, Elgar MA. The response of foraging Argentine ants, *Linepithema humile*, to disturbances. *Austr J Zoology* 2001;49:59–69.
- [68] Hantgartner W. Spezifität und Inaktivierung des Spur-pheromons von *Lasius fuliginosus* und Orientierung der Arbeiterinnen im Duftfeld. *Zeitschrift für Vergleichende Physiologie* 1967;57(2):103–6.
- [69] Helmy O, Jander R. Topochemical learning in black carpenter ants (*Camponotus pennsylvanicus*). *Ins Soc* 2003;50:32–7.
- [70] Hemelrijk C. The use of artificial-life models for the study of social organization. In: Thierry B, Singh M, Kaumanns, editors. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press; 2004.
- [71] Hölldobler B. Recruitment behaviour in *Camponotus socius*. *Zeitschrift für Vergleichende Physiologie* 1971;75:123–42.
- [72] Hölldobler B, Wilson EO. *The ants*. Cambridge: Belknap Press of Harvard University; 1990.
- [73] Jeanson R, Deneubourg JL, Grimal A, Theraulaz G. Modulation of individual behavior and Collective decision-making during aggregation site selection by the ant *Messor barbarus*. *Behav Ecol Sociobiol* 2004;55:388–94.
- [74] Jeanson R, Deneubourg JL, Theraulaz G. Discrete dragline attachment induces aggregation in spiderlings of a solitary species. *Animal Behaviour* 2004;67:531–7.
- [75] Jeanson R, Ratnieks FLW, Deneubourg JL. Pheromone trail decay rates on different substrates in the Pharaoh's ant, *Monomorium pharaonis*. *Physiological Entomology* 2003;28:1–7.
- [76] Jensen HJ. *Self-organized criticality*. Cambridge: Cambridge University Press; 1998.
- [77] Kauffman SA. *The origins of order: Self-organization and selection in evolution*. Cambridge: Oxford University Press; 1993.
- [78] Kaufman SA, Shymko R, Trabert K. Control of sequential compartment formation in *Drosophila*. *Science* 1978;199:259.
- [79] Leadbeater E, Raine NE, Chittka L. Social learning: ants and the meaning of teaching. *Current Biology* 2006;R323–5.
- [80] Le Breton J, Fourcassié V. Information transfer during recruitment in the ant *Lasius niger* L (Hymenoptera: formicidae). *Behav Ecol Sociobiol* 2004;55:242–50.
- [81] Lefever R, Lejeune O. On the origin of Tiger Bush. *Bull Math Biol* 1997;59:263–94.
- [82] Lumsden CJ, Hölldobler B. Ritualized combat and intercolony communication in ants. *J Theoret Biol* 1983;100(1):81–98.
- [83] Maillieux AC, Deneubourg JL, Detrain C. How do ants assess food volume? *Animal Behaviour* 2000;59:1061–9.
- [84] Maillieux AC, Deneubourg JL, Detrain C. How does colony growth influence communication in ants? *Insectes Sociaux* 2003;50:24–31.
- [85] Maillieux AC, Deneubourg JL, Detrain C. Regulation of ants' foraging to resource productivity. *Proc Roy Soc* 2003;270:1609–16.
- [86] Mallon EB, Franks NR. Ants estimate area using Buffon's needle. *Proc Roy Soc London* 2000;267:765–70.
- [87] Maynard Smith J. *Evolution and the theory of games*. Cambridge: Cambridge University Press; 1982.
- [88] Meinhardt H. *Models of Biological pattern formation*. NY: Academic Press; 1982.
- [89] Meinhardt H. *The algorithmic beauty of sea shells*. Berlin: Springer; 1995.
- [90] Möglich M, Maschwitz U, Hölldobler B. Tandem calling: A new kind of signal in ant communication. *Science* 1974;186:1046–7.
- [91] Moritz RF, Southwick EE. *Bees as superorganisms. An evolutionary reality*. Berlin: Springer; 1992.
- [92] Murray JD. On pattern formation for lepidopteran wing patterns and mammalian coat markings. *Philos Trans Roy Soc London B* 1981;295:473.
- [93] Murray JD. How the leopard gets its spots. *Scientific American* 1988;259:80–7.
- [94] Murray JD. *Mathematical biology. I. An introduction*. 3rd ed. Interdisciplinary applied mathematics, vol. 17. New York: Springer; 2001.
- [95] Nicolis SC, Deneubourg JL. Emerging patterns and food recruitment in ants: an analytical study. *J Theor Biol* 1999;198:575–92.
- [96] Nicolis SC, Detrain C, Demolin D, Deneubourg JL. Optimality of collective choices: a stochastic approach. *Bull Math Biol* 2003;65:795–808.
- [97] Nicolis SC, Theraulaz G, Deneubourg JL. The effect of aggregates on interaction rate in ant colonies. *Animal Behaviour* 2004;69:535–40.
- [98] Parrish JK, Hammer WM. *Animal groups in three dimensions*. Cambridge: Cambridge University Press; 1997.
- [99] Parrish J, Edelstein-Keshet L. Complexity, pattern and evolutionary trade-offs in animal aggregation. *Science* 1999;284:99–101.
- [100] Pasteels JM, Deneubourg JL, Goss S. Self-organization mechanisms in ant societies: the example of food recruitment. In: Pasteels JM, Deneubourg JL, editors. *From individual to collective behaviour in social insects*. Basel: Birkhäuser; 1987.
- [101] Portha S, Deneubourg JL, Detrain C. Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. *Behavioral Ecology* 2002;13:776–8.
- [102] Pratt SC. Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behavioral Ecology* 2005;16(2):488–96.
- [103] Rasse P, Deneubourg JL. Dynamics of nest excavation and nest size regulation of *Lasius niger* (Hymenoptera: Formicidae). *J Insect Behav* 2001;14:433–49.
- [104] Ravary F, Jahyny B, Jaisson P. Brood stimulation controls the phasic reproductive cycle of the parthenogenetic ant *Cerapachys biroi*. *Insectes Sociaux* 2006;53:20–6.
- [105] Rissing SW, Wheeler J. Foraging response of *Veromessor pergandei* to changes in seed production. *Pan-Pac Entomol* 1976;52:63–72.
- [106] Robinson EJ, Jackson DE, Holcombe M, Ratnieks FL. Insect communication: 'no entry' signal in ant foraging. *Nature* 2005;24:438–42.
- [107] Roces F. Individual complexity and self-organization of foraging by leaf-cutting ants. *Biol Bull* 2002;202:306–13.
- [108] Sakata H, Katayama N. Ant defence system: a mechanism organizing individual responses into efficient collective behaviour. *Ecological Res* 2001;16:395–403.
- [109] Sarma MS, Fuchs S, Werber C, Tautz J. Worker piping triggers hissing for coordinated colony defence in the dwarf honeybee *Apis florea*. *Zoology* 2002;105:215–23.

- [110] Schneirla TC. *Army ants: a study in social organization*. San Francisco: Freeman; 1971.
- [111] Seeley TD. *The wisdom of the hive*. Cambridge: Harvard University Press; 1995.
- [112] Shapiro JA, Dworkin M, editors. *Bacteria as multicellular organisms*. Oxford: Oxford University Press; 1997.
- [113] Sole R, Miramontes O, Goodwin B. Oscillation and chaos in ant societies. *J Theor Biol* 1993;161:343–57.
- [114] Stickland TR, Britton NF, Franks NR. Models of information flow in ant foraging: the benefits of both attractive and repulsive signals. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information Processing in Social Insects*. Basel: Birkhäuser; 1999.
- [115] Strogatz SH, Stewart I. Coupled oscillators and biological synchronization. *Scientific American* 1993;269:102–9.
- [116] Sumpter DJ. The principles of collective animal behaviour. *Phil Trans Roy Soc. London B* 2006;361:5–22.
- [117] Sumpter DJ, Beekman M. From nonlinearity to optimality: pheromone trail foraging by ants. *Animal Behaviour* 2003;66:273–80.
- [118] Sumpter DJ, Pratt SC. A modelling framework for understanding social insect foraging. *Behav Ecol Sociobiol* 2003;53:131–44.
- [119] Theraulaz G, Spitz F. *Auto-organisation et comportement*. Paris: Hermes; 1997.
- [120] Theraulaz G, Bonabeau E, Sauwens C, Deneubourg JL, Lioni A, Libert F, Passera L, Solé R. Model of droplet formation and dynamics in the Argentine ant (*Linepithema humile* Mayr). *Bull Math Biol* 2001;63:1079–93.
- [121] Theraulaz G, Bonabeau E, Nicolis SC, Sole R, Fourcassie V, Blanco S, Fournier R, Joly JL, Fernandez P, Grimal A, Dalle P, Deneubourg JL. Spatial patterns in ant colonies. *Proc Natl Acad Sci USA* 2002;99(15):9645–9.
- [122] Thierry B. In: Thierry B, Singh M, Kaumanns F, editors. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press; 2004.
- [123] Thomas ML, Framenau VW. Foraging decisions of individual workers vary with colony size in the greenhead ant *Rhytidoponera metallica* (Formicidae). *Insectes Sociaux* 2005;26–30.
- [124] Tomchik KJ, Devreotes PN. Adenosine 3', 5'-monophosphate waves in *Dictyostelium discoideum*. A demonstration by isotope dilution fluorography. *Science* 1981;212:443–6.
- [125] Traniello JF, Fujita MS, Bowen RV. Ant foraging behavior: ambient temperature affects prey selection. *Behav Ecol Sociobiol* 1984;15:65–8.
- [126] Traniello JF, Robson SK. Trail and communication in social insects. In: Bell, Cardé, editors. *The chemical ecology of insects*. London: Chapman & Hall; 1995.
- [127] Turchin S. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton, NJ: Princeton University Press; 2003.
- [128] Turing A. The chemical basis for morphogenesis. *Phil Trans Roy Soc London* 1952;237:37–72.
- [129] Verhaeghe JC. Food recruitment in *Tetramorium impurum* (Hymenoptera:formicidae). *Insectes Sociaux* 1982;29:67–85.
- [130] Vicsek T. *Fluctuations and Scaling in Biology*. Oxford: Oxford University Press; 2001.
- [131] West-Eberhard MJ. The evolution of social behavior by kin selection. *Q Rev Biol* 1975;50:1–33.
- [132] Wheeler WM. *The social insects: their origin and evolution*. London: Kegan, Treanch, Trubner & Co; 1928.
- [133] Wilson EO. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Smith): the organization of mass foraging. *Animal Behaviour* 1962;10:134–47.
- [134] Wilson EO. *The insect societies*. Cambridge, MA: Harvard University Press; 1971.
- [135] Winfree AT. Spiral waves of chemical activity. *Science* 1972;175:634–6.
- [136] Winfree AT. *The geometry of biological time*. Berlin: Springer; 1990.