Self-organization in social insects

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Self-organization was originally introduced in the context of physics and chemistry to describe how microscopic processes give rise to macroscopic structures in out-of-equilibrium systems. Recent research, that extends this concept to ethology, suggests that it provides a concise description of a wide range of collective phenomena in animals, especially in social insects. This description does not rely on individual complexity to account for complex spatiotemporal features which emerge at the colony level, but rather assumes that interactions among simple individuals can produce highly structured collective behaviours.

Many collective activities performed by social insects result in complex spatiotemporal patterns. Ethologists are often tempted to assume that such complex patterns at the colony level can be generated only by complex individuals, that is, by individuals who are able to take into account numerous parameters to modulate their behaviours. Theories of self-organization (SO), originally developed in the context of physics and chemistry to describe the emergence of macroscopic patterns out of processes and interactions defined at the microscopic level[1,2], can be extended to ethological systems, particularly social insects, to show that complex collective behaviours may emerge from interactions among individuals that exhibit simple behaviours: in these cases, there is no need to invoke individual complexity. Recent research shows that SO is indeed a major component of a wide range of collective phenomena in social insects[3]. But work on SO in insect societies, and more generally in ethology, is easily overlooked because the emphasis of SO is on how[4] collective behaviours causally result from the individual level: SO does not explicitly deal with the complementary question of why collective patterns of activity appeared in the course of evolution. Nevertheless, we believe it both

worthwhile and important to understand the proximate mechanisms that have evolved through natural selection and may have affected the evolutionary path[5]. Discussing evolutionary issues without understanding how behaviours are actually implemented and what parameters may influence them may become a dangerous abstraction.

Self-organization in insect societies

SO can be applied to the study of various aspects of social life in insects. A choice between two equivalent food sources by ants can be performed collectively by means of SO: foragers are initially evenly distributed between the two sources, but one of the sources randomly becomes slightly favoured, and this difference may be amplified by recruitment, since the more foragers there are at a given source, the more individuals recruited to that source, especially if pheromone trails are involved[3]. When a source is richer, foragers exploiting this source lay more trail than those exploiting the poorer source, leading the colony to select the richer source[3]. Similarly, the interplay between recruitment and travel time or individual orientational memory[6], leads to the collective selection of the shortest path, as evidenced by a related experiment, where the nest is separated from a single food source by a bridge with two branches (Box 1).

In bees, food source selection relies, not on chemical trails, but on recruitment through dances. Box 2 indicates how a model based on SO can accurately account for experimentally observed behaviours in honeybees[7]. It has been argued[8] that SO is also at work in the development of the characteristic pattern of brood, pollen and

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honey on the combs of honeybee colonies (Box 3).

SO can help describe many aspects of building activities[9-11]. In this context, it is often combined with the mechanism of stigmergy. Stigmergy is a notion introduced by Grassé[12,13] to describe the indirect communication taking place among individual termites through dynamically evolving features of a structure: a stimulating configuration triggers a building action by a termite worker, which transforms the configuration into another configuration that may in turn trigger another (possibly different) action performed by the same termite or any other worker. Stigmergy can be contrasted with recipes, where a set of instructions specifies a sequence of behaviours[14]. Such a rigid behavioural program unfolding in time without any feedback from the structure being built can be appropriate for solitary animals, but makes coordination difficult. One important problem with stigmergy is understanding how stimuli are organized in space and time to ensure a coherent building. Deneubourg[9] showed that chemical cues could organize part of the building activities of termites through a self-organizing stigmergic process (Box 4). In this case, the stimuli encountered by the termites (concentrations of construction pheromones) differ quantitatively. There seem to be other cases where the stimulating patterns of matter perceived by the insects, such as wasps, undergo qualitative changes[15-17].

Other examples where SO can, at least partially, describe the collective activities of social insects, include the formation of trail networks and foraging patterns in many ant species[3,6,18,19], rhythmical patterns of activity in ants (*Leptothorax*)[20,21], large prey carrying in ants[22], thermoregulation in clusters of bees[23], the piling of dead bodies by ants (*Pheidole*)[24], larval sorting by ants (*Leptothorax*)[24], or the dynamics of

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colony development in wasps (*Polistes*)[25]. SO has also been applied to the modelling of the social organization, including hierarchical differentiation[26-28] (the more an individual wins, the more likely it is to win), division of labor[26] (the more a task is performed by a given individual, the more likely is the individual to perform this task; see also Ref. 29), and age (or temporal) polyethism[30]: such models are generally more speculative in nature, because of a lack of a clear understanding of the mechanisms underlying the phenomena, but they deserve attention in that they constitute plausible explanations complementing classical theories. Finally, ethological applications of SO are certainly not restricted to insect societies. For example, many arthropod societies possess coordinated group-expressed behaviours, like cooperative foraging in some caterpillar societies[31], or group hunting in 'social' spiders[32].

Definition and properties of SO

On the basis of the examples given in the previous section, and described in Boxes 1, 2, 3, and 4, we can now define SO as a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among its lower-level components[1,2]. The rules specifying the interactions among the system's constituent units are executed on the basis of purely local information, without reference to the global pattern, which is an emergent property of the system rather than a property imposed upon the system by an external ordering influence. For example, the emerging structures in the case of foraging in ants include spatio-temporally organized networks of pheromone trails. But how do such structures emerge?

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The basic ingredients of SO[1,2]

(1) Positive feedback (amplification) often constitutes the basis of morphogenesis in the context of this paper: they are simple behavioural 'rules of thumb' that promote the creation of structures. Examples of positive feedback include recruitment and reinforcement. For instance, recruitment to a food source is a positive feedback that relies on trail laying and trail following in some ant species, or dances in bees.

(2) Negative feedback counterbalances positive feedback and helps to stabilize the collective pattern: it may take the form of saturation, exhaustion or competition. In the example of foraging, negative feedback stems from the limited number of available foragers, satiation, food source exhaustion, crowding at the food source, or competition between food sources.

(3) SO relies on the amplification of fluctuations (random walks, errors, random task-switching, and so on). Not only do structures emerge despite randomness, but randomness is often crucial, since it enables the discovery of new solutions, and fluctuations can act as seeds from which structures nucleate and grow.

(4) All cases of SO rely on multiple interactions. A single individual can generate a self-organized structure such as a stable trail provided pheromonal lifetime is sufficient, because trail-following events can then interact with trail-laying actions. However, SO generally requires a minimal density of mutually tolerant individuals. Moreover, individuals should be able to make use of the results of their own activities as well as of others' activities (although they may perceive the difference): for instance, trail networks can self-organize and be used collectively if individuals use others' pheromone. This does not exclude the existence of individual chemical signatures or individual memory which can efficiently complement or sometimes replace responses to collective marks[6].

Signatures[1,2]

The characteristic signatures of SO include:

(1) The creation of spatiotemporal structures in an initially homogeneous medium.

(2) The possible coexistence of several stable states (multistability): Because structures emerge by amplification of random deviations, any such deviation can be amplified, and the system converges to one among several possible stable states, depending on initial conditions.

(3) The existence of bifurcations when some parameters are varied: The behaviour of a self-organized system changes dramatically at bifurcations. For example, pillars built by termites can emerge only if there is a critical density of termites. The system undergoes a bifurcation at this critical number: no pillar emerges below it, but pillars can emerge above it (Box 4).

Alternative mechanisms

SO is not a universal mechanism. Other mechanisms can shape collective activities. For instance, the organization of some activities, such as worker foraging in wasps[33], has been interpreted as resulting from active regulation and control by the queen, the central organizer of a large amount of information which is redistributed to the workers through stimulations. Another possible mechanism is the use of a template: the shape to be built 'already exists' under the form of a prepattern in the environment. This prepattern can result from natural gradients, fields or heterogeneities that are exploited by the colony. Many ant species (including *Acantholepsis custodiens*[34], *Formica polyctena* and *Myrmica rubra*[35]) make use of temperature and humidity gradients to build their nests and spatially distribute eggs, larvae and pupae. The prepattern can also be the body shape of an animal, as

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illustrated by the example of the construction of the royal chamber in termites (*Macrotermes subhyalinus*) (see Box 5)[13]. Other factors, such as genetically determined response thresholds, also play an important role in shaping individual behaviour[36]. These factors can sometimes be combined with SO. For example, we have assumed for clarity throughout this paper that all individuals in the colony are identical units: this inaccurate view of reality served our purpose in showing that complex patterns can emerge in populations of simple interacting identical individuals. SO does not, however, require identical individuals and can work, possibly even more efficiently, when individuals belong to different castes or have different response thresholds to pheromone trails or to other stimuli: in this latter case, SO can make use of these different thresholds to organize collective behaviours[26,36].

Self-organization and evolution

Models based on SO are aimed at elucidating the proximate mechanisms that allow the emergence of collective structures. They do not deal explicitly with the question of why such collective structures and their associated self-organized mechanisms appeared in the course of evolution. In that respect, SO does not contradict but rather complements theories of evolution, and must not be considered as an argument in favour of any specific theory (such as group selection theory[37]) because it does not focus on the same issues. It is clear, however, that evolution has had to deal with 'implementation issues'[4,5,38]. Recognizing the importance of SO as a major set of organizing mechanisms, and understanding how SO may be at work in many instances of collective behaviours will allow a better understanding of evolution itself.

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How does selection operate on self-organizing phenotypes?

Selection can operate on parameters or factors that influence colony-level structures, be these self-organized or not[39,40]. Such factors include response thresholds to stimuli, the behavioural output resulting from these stimuli, or specific properties of chemicals used as alarm, construction or trail pheromones: changing these factors undoubtedly changes global patterns and the conditions under which they can emerge and be maintained. For example, the volatility of a pheromone can affect foraging trails: obviously, this property is essential in defining the efficiency of a colony in a given environment, and may have coevolved with other features, such as colony size[3], since a volatile trail pheromone requires more individuals to maintain stable trails.

Self-organized systems are not necessarily adaptive[40] or even cooperative (the very notion of cooperation is absent when SO occurs in physical or chemical systems), but natural selection, operating on parameters that modulate individual and colony-level properties, has certainly picked the forms of self-organization that we see in social insects because they are adaptive or cooperative[39,40]. In particular, in the examples treated in this article, SO is associated with emergent adaptive and/or cooperative phenomena.

Some self-organizing strategies may be favoured by evolution.

• Specific self-organizing strategies may have appeared in the first place because of the underlying simplicity of their behavioural mechanisms and because of the relatively weak conditions required for their emergence. Their subsequent selection depended on their efficiency relative to the environment in which they emerged.

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• Evolution can favour self-organizing strategies that take advantage of existing biological implementations or mechanisms. For instance, a species of ant can be capable of piling seeds, larvae, and dead bodies by means of SO[24,41,42]: whereas the processes of recognition involved in each of these different activities certainly rely on different signals, the logical mechanisms of attraction and amplification that lead to piles and clusters are very similar. Another example is the absence of any clear-cut distinction between pheromones involved in space exploration, food recruitment and defence recruitment (territorial marking) in many ant species[43]: here, both the logical mechanisms (trail laying-trail following) and the signals (pheromones) are similar in these different activities.

• Another reason why SO may be widespread is that the same individual level behaviours may be used to generate different collective responses in different environments. For example, Franks et al. [19] have shown with a combination of computer simulations and field experiments that the different exploratory patterns of army ants species could result from different spatial distributions of their prey and not necessarily from differences in individual behaviours. These simulations do not imply that individuals of all species of army ants have exactly the same behaviour, but suggest that behavioural rules may be qualitatively similar in all species, possibly because of common ancestors: evolution may then have modulated these rules quantitatively (by changing response thresholds or specific chemicals).

It appears therefore that SO may have been favoured by evolution since it facilitates the emergence of efficient collective patterns and does not require complex individuals. However, the question of how SO and evolution interact is still largely

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open, not only in insect societies but in ecology, ethology and biology in general[38].

Conclusion

The organization of insect societies can be better understood using experimental and theoretical approaches based on SO. If current research is aimed at showing the existence of self-organizing processes in social insects, future work should undertake the study of such proximate mechanisms in a broad evolutionary perspective that would in turn be enriched by the inclusion of knowledge about proximate causes.

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References

1   Haken, H. (1977) *Synergetics*, Springer-Verlag

2   Nicolis, G. and Prigogine, I. (1977) *Self-organization in non-equilibrium systems*, Wiley

3   Deneubourg, J-L. and Goss, S. (1989) **Collective patterns and decision making,** *Ethol. Ecol. Evol.* 1, 295-311

4   Tinbergen, N. (1963) *The Herring Gull's World. A Study of the Social Behaviour of Birds*, Collins

5   Mangel, M. (1995) **Social interactions, nonlinear dynamics and task allocation in groups,** *Trends Ecol. Evol.* 10, 347

6   Beckers, R., Deneubourg, J-L. and Goss, S. (1992) **Trails and U-turns in the selection of a path by the ant** *Lasius niger, J. Theor. Biol.* 159, 397-415

7   Camazine, S. and Sneyd, J. (1991) **A model of collective nectar source selection by honey bees: self-organization through simple rules,** *J. Theor. Biol.* 149, 547-571

8   Camazine, S. (1991) **Self-organizing pattern-formation on the combs of honeybee colonies,** *Behav. Ecol. Sociobiol.* 28, 61-76

9   Deneubourg, J.L. (1977) **Application de l'ordre par fluctuations à la description de certaines étapes de la construction du nid chez les termites,** *Insect. Soc.* 24, 117-130

10 Karsai, I. and Penzes, Z. (1993) **Comb building in social wasps: self-organization**

and stigmergic script, *J. Theor. Biol.* 161, 505-525

11   Skarka, V., Deneubourg, J-L. and Belic, M.R. (1990) **Mathematical model of building behavior of** *Apis mellifera. J. Theor. Biol.* 147, 1-16

12   Grassé, P.-P. (1959) **La reconstruction du nid et les coordinations inter- individuelles chez** *Bellicositermes Natalensis et Cubitermes sp.* **La théoriede la stigmergie: essai d'interprétation du comportement des termites constructeurs,** *Insect. Soc.* 6, 41-84

13   Bruinsma, O. H. (1979) **An analysis of building behaviour of the termite** *Macrotermes subhyalinus* **(Rambur),** PhD Thesis, Landbouwhogeschool, Wageningen, The Netherlands.

14   Eibl-Eibesfeldt, I. (1970) *Ethology: The Biology of Behaviour* , Holt, Rinehart & Winston

15   Karsai, I. and Theraulaz, G. (1995) **Nest building in a social wasp: Postures and constraints,** *Sociobiology* 26, 83-114

16   Downing, H. A. and Jeanne, R. L. (1988) **Nest construction by the paperwasp** *Polistes***: A test of stigmergy theory,** *Anim. Behav.* 36, 1729-1739

17   Theraulaz, G. and Bonabeau, E. (1995) **Coordination in distributed building,** *Science* 269, 686-688

18   Edelstein-Keshet, L., Watmough, J. and Ermentrout, G.B. (1995) **Trail following in ants: individual properties determine population behaviour,** *Behav. Ecol. Sociobiol.* 36, 119-133

19   Franks, N. R. *et al.* (1991) **The blind leading the blind in army ant raid patterns — testing a model of self-   organization,** *J. Insect Behav.* 4, 583-607

20   Cole, B. J. (1991) **Short-term activity cycles in ants: generation of periodicity by worker interaction,** *Am. Nat.* 137, 244

21   Franks, N. R., Bryant, S., Griffiths, R. and Hemerik, L. (1990) **Synchronization of**

the behaviour within nests of the ant *Leptothorax acervorum* (Fabricius) — I. Discovering the phenomenon and its relation to the level of starvation, *Bull. Math. Biol.* 52, 597-612

22 Detrain, C. and Deneubourg, J-L. Scavenging by *Pheidole pallidula*: A key for understanding decision-making systems in ants, *Anim. Behav.* (in press)

23 Watmough, J. and Camazine, S. (1995) **Thermoregulation of honeybee clusters**, *J. Theor. Biol.* 176, 391-402

24 Deneubourg, J-L. *et al.* (1991) **The dynamics of collective sorting : Robot-like ant and ant-like robot**, in *From Animals to Animats* (Meyer, J.A. and Wilson, S.W., eds), pp. 356-365, MIT Press

25 Karsai, I., Penzes, Z. and Wenzel, J. W. (1996) **Dynamics of colony development in Polistes dominulus: a modeling approach**, *Behav. Ecol. Sociobiol.* 39, 97-105

26 Theraulaz G. *et al.* (1991) **Task differentiation in Polistes wasp colonies: a model for self-organizing groups of robots**, in *From Animals to Animats* (Meyer, J.A. and Wilson, S.W., eds), pp. 346-355, MIT Press

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

28 Hogeweg, P. and Hesper, B. (1985) **Socioinformatic processes: MIRROR modelling methodology**, *J. Theor. Biol.* 113, 311-330

29 Pacala, S. W., Gordon, D. M. and Godfray, H. C. J. (1996) **Effects of social group size on information transfer and task allocation**, *Evol. Ecol.* 10, 127 165

30 Tofts, C. and Franks, N. R. (1994) **Foraging for work: how tasks allocate workers**, *Anim. Behav.* 48, 470-472

31 Fitzgerald, T. D. (1995) *The tent caterpillars*, Cornell University Press

32 Krafft, B. and Pasquet, A. (1991) **Synchronized and rhytmical activity during**

prey capture in the social spider *Anelosimus eximius* (Araneae, Theridiidae), *Insect. Soc.* 38, 83-90

33 Reeve, H. K. and Gamboa, G. J. (1987) **Queen regulation of worker foraging in paper wasps: A social feedback control system** (*Polistes fuscatus*, Hymenoptera: Vespidae), *Behaviour* 102, 147-167

34 Brian, M.V. (1983) *Social Insects: Ecology and Behavioural Biology*, Chapman & Hall

35 Ceusters, R. (1986) **Simulation du nid naturel des fourmis par des nids artificiels placés sur un gradient de température**, *Actes Coll. Insect. Soc.* 3, 235-241

36 Bonabeau, E., Theraulaz, G. and Deneubourg, J-L. (1996) **Quantitative study of the fixed threshold model for the regulation of division of labor in insect societies**, *Proc. Roy. Soc. London Ser. B* 263, 1565-1569

37 Wynne-Edwards, V.C. (1993) **A rationale for group selection**, *J. Theor. Biol.* 162, 1-22

38 Kauffman, S. A. (1993) *The Origins of Order*, Oxford University Press

39 Bourke, A. F. G. and Franks, N. R. (1995) *Social Evolution in Ants*, Princeton University Press

40 Reeve, H. K. and Sherman, P. W. (1993) **Adaptation and the goals of evolutionary research**, *Quart. Rev. Biol.* 68, 1-32

41 Detrain, C. and Pasteels, J.M. (1991) **Caste differences in behavioral thresholds as a basis for polyethism during food recruitment in the ant** *Pheidole pallidula* (Nyl.) (Hymenoptera: Myrmicinae), *J. Insect Behav.* 4, 157-176

42 Hölldobler, B. and Wilson, E.O. (1978) **The multiple recruitment systems of the African weaver ants** *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae), *Behav. Ecol. Sociobiol.* 3, 19-60

43   Aron, S. *et al.* (1993) **Memory and chemical communication in the orientation of two mass-recruiting ant species,** *Insect. Soc.* **40,** 369-380

Box 1. Foraging in ants

In experiments with *Linepithema humile* and *Lasius niger*, a food source is separated from the nest by a bridge with two equally long branches A and B (Fig. 1a). Initially, both branches have the same probability of being selected: choices are made at random. But a few more ants randomly select branch A, where they deposit pheromone. The greater amount of pheromone on A stimulates more ants to choose A, and so on[1] . When the bridge's branches are not the same length, the shorter branch is selected more frequently by the same mechanism (the amplification of initial fluctuations): the first ants returning to the nest take the shorter path twice (from the nest to the source and back), and therefore influence outgoing ants towards the short branch. However, this mechanism does not allow switching to the shorter branch if it is presented after the longer one, because the first presented branch has become too strongly marked. With *Lasius niger*, another mechanism allows the selection of the shorter path. When it finds itself in the middle of the long branch, this ant often realizes that it is heading almost perpendicularly to the required direction: this induces it to make a high proportion of U-turns on the long branch[9]. In this case, the combination of individual memory for the direction to the nest or food source, plus collective trail following allows the systematic selection of the short branch (Fig. 1b).
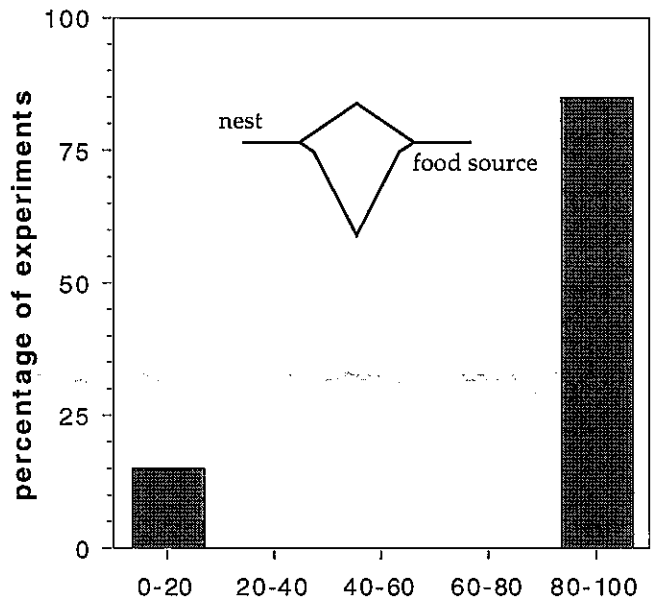

Insert figure 1

(a)
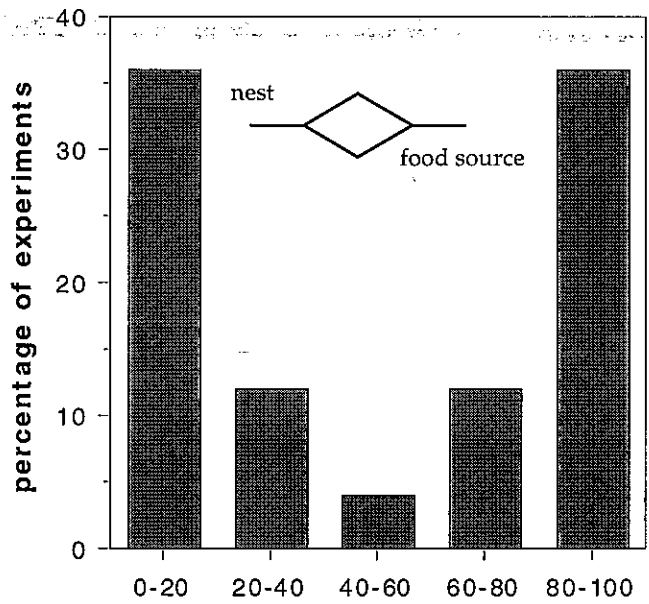
percentage of traffic on an arbitrary branch
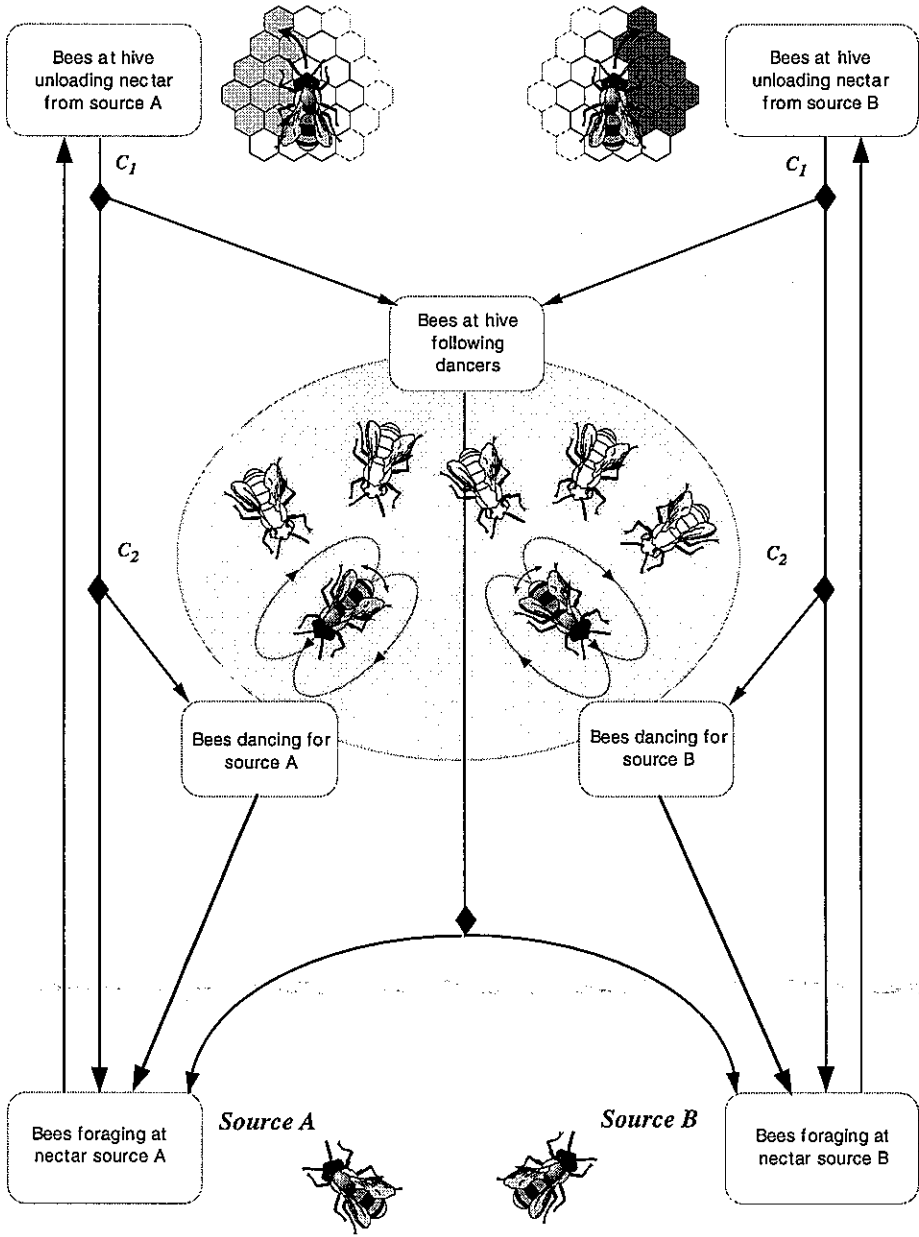
(b)

percentage of traffic on short branch

Box 2. Foraging in bees

When a bee finds a nectar source, she goes back to the hive and relinquishes her nectar to a hive bee. Then she can either start to dance to indicate to other bees the direction and the distance to the food source, or continue to forage at the food source without recruiting nestmates, or she can abandon her food source and become an uncommitted follower herself. If the colony is offered two identical food sources at the same distance from the nest, the bees exploit the two sources symmetrically. It has been shown experimentally that a bee has a relatively high probability of dancing for a good food source and abandoning a poor food source. These simple behavioural rules allow the colony to select the better quality source. Camazine *et al.*[7] have confirmed with a simple mathematical model based on these observations that foragers can home in on the best food source through a positive feedback created by differential rates of dancing and abandonment based upon nectar source quality. The figure shows a schematic representation of foraging activity; decision points (C_1: become a follower?) and (C_2: become a dancer?) are indicated by black diamonds.

Insert figure 2

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Bees at hive
unloading nectar
from source A

Bees at hive
unloading nectar
from source B

C_1

C_1

Bees at hive
following
dancers

C_2

C_2

Bees dancing for
source A

Bees dancing for
source B

Bees foraging at
nectar source A

Source A

Source B

Bees foraging at
nectar source B

# Box 3. Self-organization on the combs of honeybee colonies

A characteristic well-organized pattern develops on the combs of honeybee colonies. This pattern consists of three concentric regions (a central brood area, a surrounding rim of pollen, and a large peripheral region of honey). It results to a large extent from a self-organized process based on local information[8]. The model relies on the following assumptions, suggested by experimental observations:

(1) The queen moves more or less randomly over the combs and lays most eggs in the neighbourhood of cells already occupied by brood. Eggs remain in place for 21 days.

(2) Honey and pollen are deposited in randomly selected available cells.

(3) Four times more honey is brought back to the hive than pollen.

(4) Typical removal:input ratios for honey and pollen are 0.6 and 0.95, respectively.

(5) Removal of honey and pollen is proportional to the number of surrounding cells containing brood.

Simulations of a cellular automaton based on these rules were performed[8]. Figure 3 shows four successive steps in the formation of the concentric regions of brood (grey circles), pollen (red circles) and honey (yellow circles). Rules (1) and (5) ensure the growth of a central compact brood area if the first eggs are laid approximately at the center of the comb. Honey and pollen are initially randomly mixed [rule (2)], but

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rules (3) and (4) imply that pollen cells are more likely to be emptied and refilled with honey, so that pollen located in the periphery is removed and replaced by honey. The only cells available for pollen are those surrounding the brood area, because they have a high turnover rate. The adaptive function of this pattern is discussed in Ref. 8.

Insert figure 3
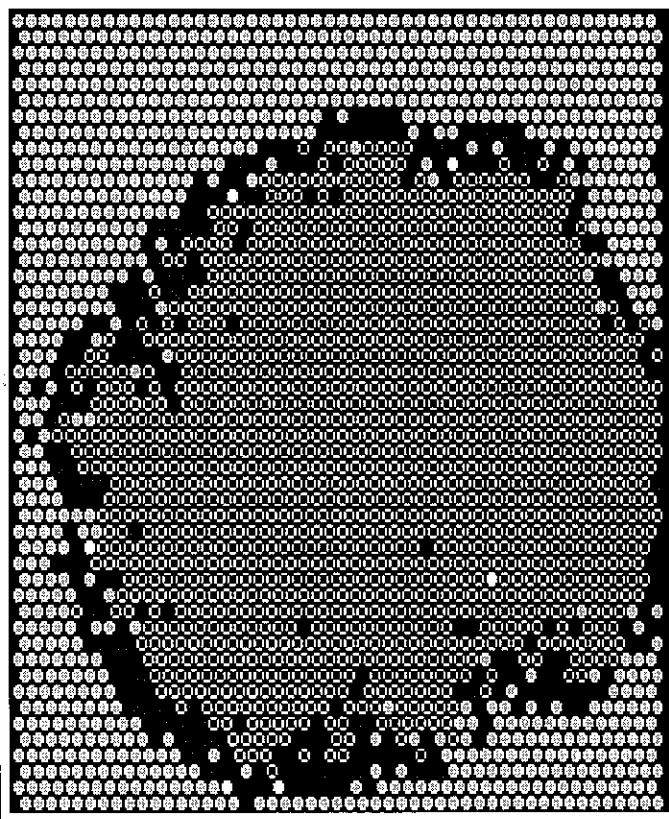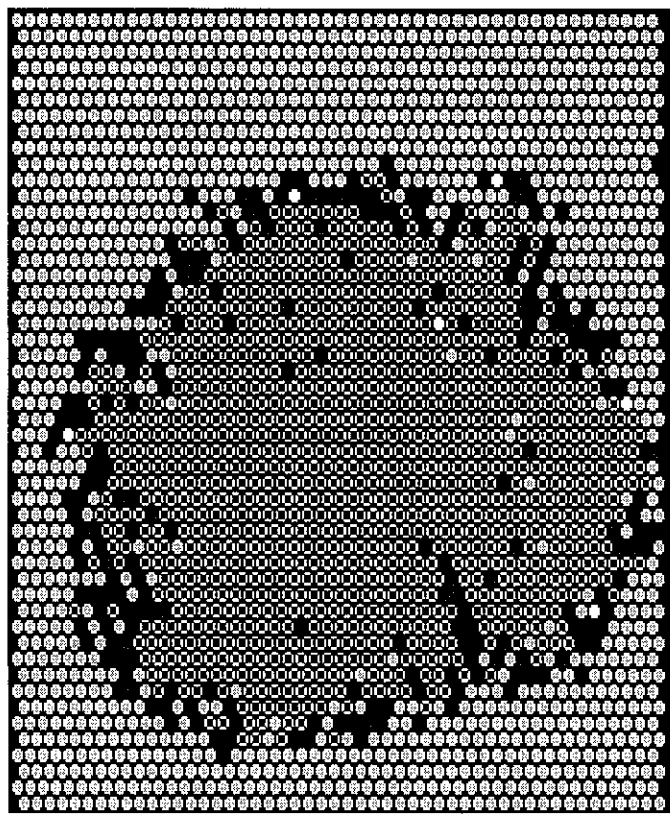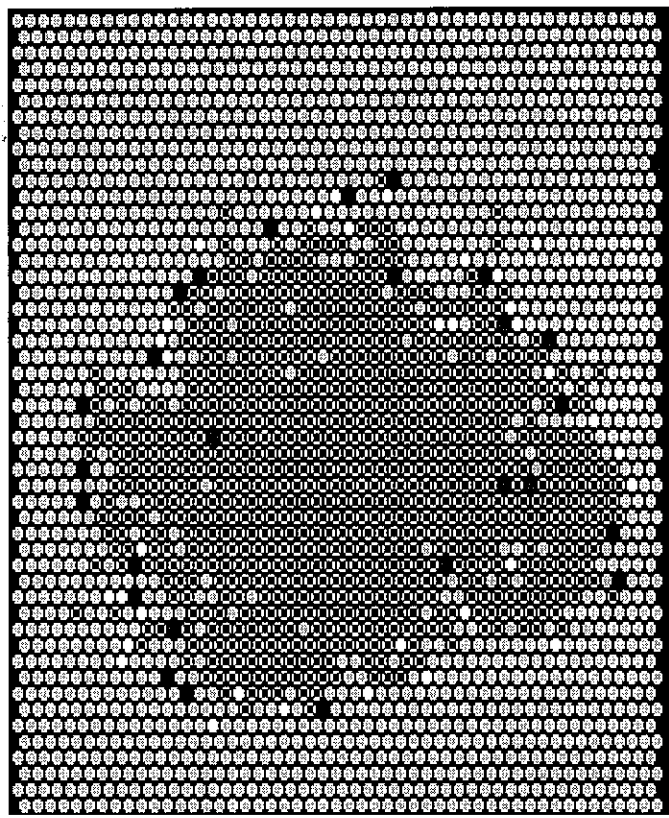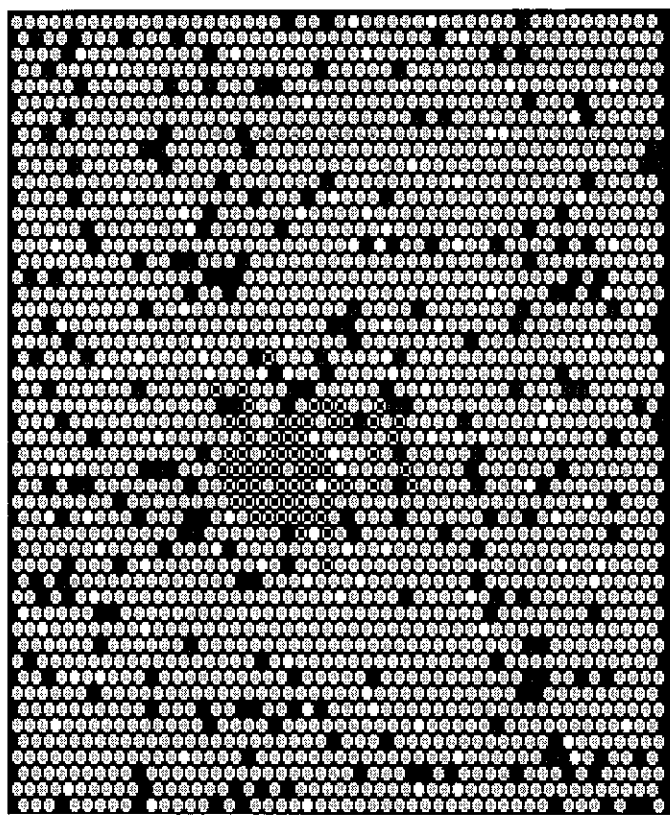
Box 4. Stigmergy in the construction of pillars by termites

The termite *Macrotermes* uses soil pellets impregnated with pheromone to build pillars (Fig. 4). Two successive phases take place[12]. First, the non-coordinated phase is characterized by a random deposition of pellets. This phase lasts until one of the deposits reaches a critical size. Then, the coordination phase starts if the group of builders is sufficiently large: pillars or strips emerge. The existence of an initial deposit of soil pellets stimulates workers to accumulate more material through a positive feedback mechanism, since the accumulation of material reinforces the attractivity of deposits through the diffusing pheromone emitted by the pellets[13]. This autocatalytic, 'snowball effect' leads to the coordinated phase. If the number of builders is too small, the pheromone disappears between two successive passages by the workers, and the amplification mechanism cannot work; only the non-coordinated phase is observed. There is therefore no need to invoke a change of behaviour by the participants in the transition from the non-coordinated to the coordinated phase: it is merely the result of an increase in group size.
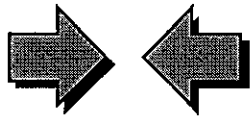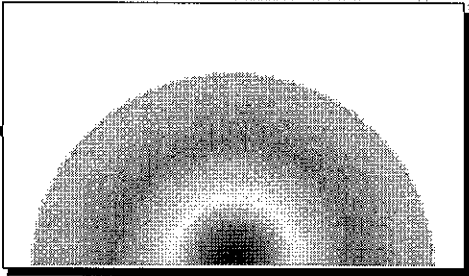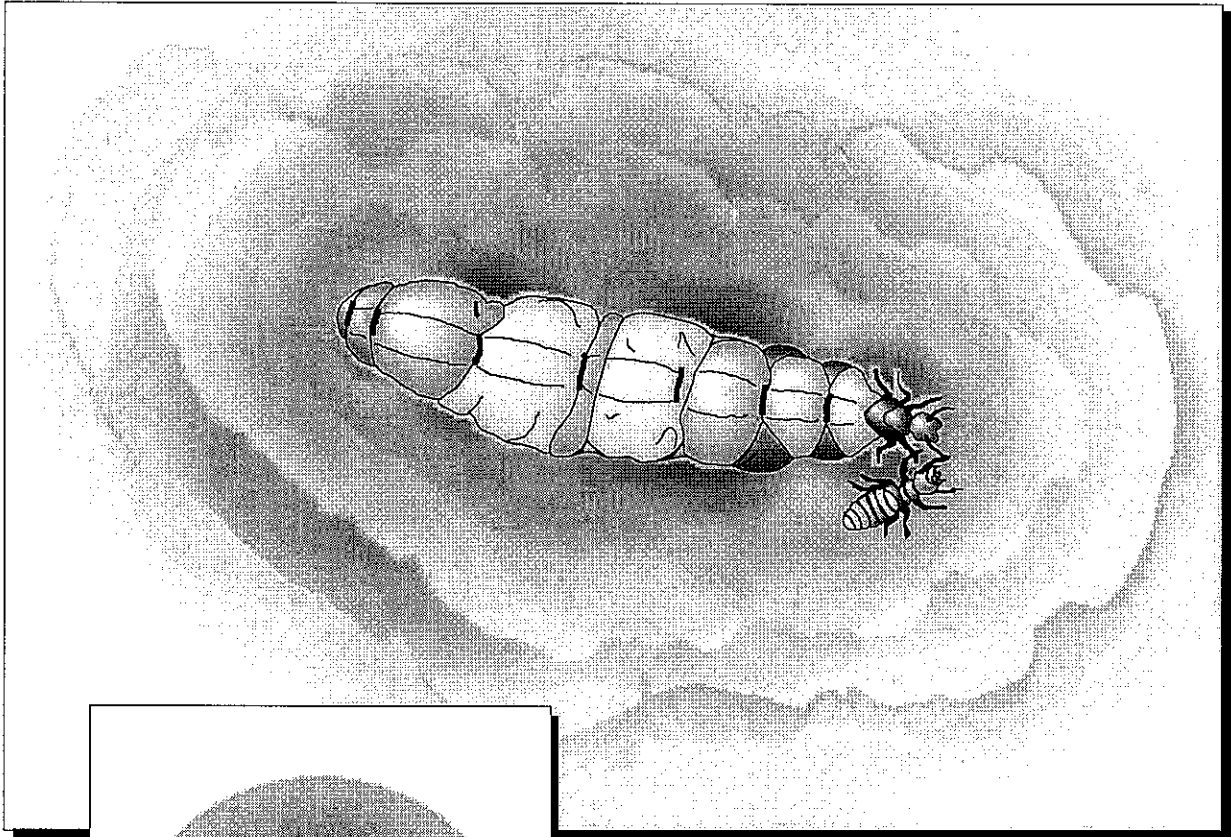
Insert figure 4

A_3 → R_3 (any individual)

A_2 → R_2 (any individual)

A_1 → R_1 (any individual)

A → R (Individual S)
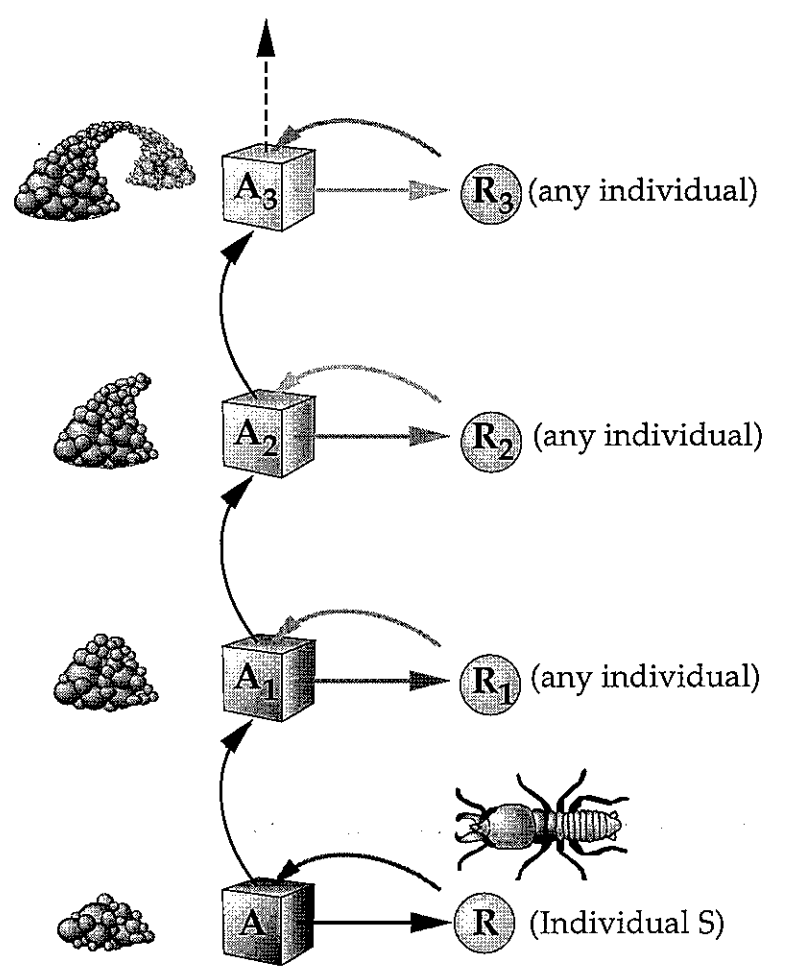
Box 5. Example of a template: the construction of the royal chamber in termites

The physogastric queen of *Macrotermes subhyalinus* emits a pheromone that diffuses and creates a pheromonal template in the form of a decreasing gradient around her (see figure below). It has been shown experimentally that a concentration window exists, or a threshold, that controls the workers' building activities: a worker deposits a soil pellet if the concentration of pheromone is within this window or exceeds the threshold[13]. Otherwise, they do not deposit any pellet or even destroy existing walls. If one places a freshly killed physogastric queen in various positions, walls are built at a more or less constant distance from the queen's body, following its contours, while a wax dummy of the queen does not stimulate construction. In this description, we have omitted for simplicity tactile stimuli and other pheromones, such as cement and trail pheromones, that facilitate the recruitment, coordination and orientation of individual workers, and that determine the detailed shape of the reconstructed chamber: the major organizing role is played by the queen's building pheromone which creates a chemical template. Notice that in contrast with SO, the production of patterns based on templates does not require a critical number of individuals, and does not exhibit multistability.

Insert figure 5

C_{max} C_{min}