1 Self-organization and Stigmergy

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14 Self-organization refers to processes of pattern formation based on local interactions among
15 the individuals without explicit reference to the collective behavior of the whole society or to
16 external control [5]. These interactions may be mediated by information exchange among
17 individuals or by the byproducts of their activity, with the emerging structure itself inducing a
18 specific behavior of the group members. We will illustrate this concept by examples drawn
19 from social insects. These include nest building, collective foraging, temporal synchronicity,
20 collective choices, and division of labor. Finally, we introduce the notion of non-linearity that
21 is at the basis of self-organized processes. In particular, we develop an analysis of different
22 foraging strategies based on individual foraging, group recruitment or trail recruitment, to
23 progressively introduce the concepts of non-linear response, amplification, and multiple
24 stationary states.

25 Nature provides a range of strikingly regular structures, such as the regular pattern of
26 ripples on sand dunes, the pigmentation pattern on shells, and the synchronized movements
27 of bird flocks [1]. A common feature of these physical and biological systems is the self-
28 organized way by which they acquire structure. Self-organization refers to processes of
29 pattern formation in which structures develop through interactions among the system
30 components without external control [22]. In self-organized biological systems, the
31 components can be molecules, cells or individuals that generate adaptive structures at a
32 higher organizational level. These structures emerge without reference to an external
33 template, procedure or pre-established plan.

34 In the case of social animals, the patterns of foraging trails, the architecture of nests or
35 the social organization of work can arise from multiple interactions among group-mates, even
36 though each individual has access only to local information and is not aware of the emerging
37 global pattern. An amazing diversity and complexity of collective structures can then arise
38 from rather simple behavioral rules followed by the individuals [10].

39 In such self-organized collective responses, the interactions between nestmates are
40 mediated by direct communication through signals or by indirect cues left by the individuals.
41 In many cases, direct interactions involve tactile, visual, auditory or chemical signals that are
42 specifically emitted to transfer information to other group members. The formation of the

collective pattern is closely related to the number of individuals that concurrently interact as well as to the intensity of the exchanged signals [14].

Indeed, because interactions among group-mates form the basis of these self-organized behaviors, any parameters that can impact the rate of interactions (e.g. the local density of workers, their absolute number, or the intensity of the exchanged signals) will influence the final patterns emerging at the collective level. In the genesis of some self-organized structures, each individual responds to local changes in its environment, such changes being byproducts of the activity of the nestmates. Interactions between group-members are thus indirect, and coordination takes place via a shared environment. This latter structuring process is often referred as stigmergy. These stigmergy-based structures only depend on the current state of the environment. They can emerge without direct coordination among group members and may even result from the actions of a single individual.

Characteristics of self-organized systems

Self-organization underlies various collective activities (e.g. foraging, nest building, defense) in a wide range of organisms. These include bacteria, invertebrates (e.g. locusts, ants, honey bees, termites) and vertebrates (e.g. birds, fish, mammals) including humans [5, 9, 26]. The ubiquity of self-organized processes illustrates their high potential to create structure within any group of interacting animals, providing that they show some biological predispositions. In the first place, the underlying behaviors or/and interactions between nestmates must be self-amplifying to allow their propagation inside the group. For instance, information-laden signals emitted by one individual should stimulate the receiver to express a specific behavioral response and, in turn, produce a signal identical to the one he received. Such positive feedback loops will ultimately lead to the propagation of information and/or behavior in the whole group of interacting nestmates. This positive feedback is often dependent on a critical colony size, nestmate density or activity level that has to be reached, in such a way that the rate of interactions will be high enough to initiate collective dynamics of pattern formation.

Although positive feedback is central to pattern formation, it may lead to uncontrollable processes or amorphous structures if not coupled to negative feedback that slows the amplifying dynamics in motion. The snowballing effect can be kept under control by negative feedback such as the fading out of the amplifying signal or a limitation in the number of individuals that can be activated. It is the balance between positive and negative feedback that will determine the structure towards which the social system will evolve.

How self-organized responses change over time is not entirely predictable. It is often possible to foresee the emergence of a structure, but it can be difficult to predict its exact location or the timing of its appearance. However, we can find statistical regularities in the quantitative features of self-organized phenomena (e.g. the number of cooperating foragers, the number of individuals under a specific shelter, the connectivity of the chambers in an ant nest). In this respect, modelling tools allow us to trace step-by-step the dynamics of the social response. For instance, one can design simulations that iteratively apply the rules governing the interactions between individuals, take into account random variations and then unveil the possible emerging structures. Mathematical modelling and simulations thus appeared to be indispensable tools to tackle the complexity of self-organized collective responses.

Alternatives to self-organization

Self-organization is involved in a wide range of collective behaviors, but it is important to keep in mind alternative mechanisms of pattern formation, such as leadership, stimulus-response recipes or templates. First, an informed individual may act as a leader by steering and controlling the activity of its fellows. Unlike self-organized activities that are quite resilient to the removal of some workers, a leadership-based collective behavior is highly sensitive to the removal of these key-individuals. For instance, in some ant species, blocking the interactions between a leader and her follower will prevent the moving of the whole colony to a new nest or the collective exploitation of a new food source.

Second, workers may possess a recipe (i.e. a fixed stimulus-response sequence) to guide them step-by-step until the final pattern is completed. Instead of adjusting their behavior based on the emerging structure (stigmergy), these recipe-driven insects will continue their stereotyped behavioral sequence despite the emergence of non-functional structures.

The last alternative is the use of a template that determines the shape and the size of the built-pattern. For example, the body size of the termite sexuals -- more precisely the chemical gradient of compounds emitted by the queen -- defines the distance at which material is laid to build the walls of the royal chamber. Another example of template can be found in the case of ants where the level of carbon-dioxide inside the nest influences the spatial organization of workers.

Self-organization and stigmergy in social insects

While such processes are observed across several taxa, self-organization is prominent and widespread in the collective behavior of social insects [18]. The diversity of collective responses that can be generated without assuming complex behavior or high cognitive abilities at the individual level have made self-organization the backbone of many insect societies [3]. Typically, self-organization meets the parsimony principle (Ockham's razor) that demands an economy of hypotheses to account for complex phenomena. By coupling behavioral experiments to theoretical simulations, in which agents are designed to behave like insects, we can assess the relative importance of self-organizing processes and identify key values of biological parameters involved in pattern formation. As for any other kinds of biological phenomena, self-organized patterns in insect societies depend on physiological and behavioral interactions that have been selected throughout evolution. Natural selection has caused the retention of a subset of the collective patterns that can potentially emerge and that will allow the whole society to respond to environmental challenges. The key role of self-organization is well-demonstrated in (among others) nest building, food harvesting and division of labor (Fig. 1).

Figure 1. Examples of self-organized behaviors and structures in social insects. A. A **macrotermitinae** mound nest. Photo by Joe Tarafdar, Wikimedia Commons. B. The regular hexagonal cells in a honey bee comb. Photo by Piscisgate, Wikimedia Commons. C. Ants following a common chemical trail formed on a concrete walkway. Photo by Fanghong, Wikimedia Commons. D. A physically marked trunk trail formed by the repeated passages of the foragers of an ant colony. Photo by Fir0002, Wikimedia Commons. E. Synchronization of the activity level among nestmates. In this simulated example, five workers progressively coordinate their activity level by mutual influence on the phase and frequency of their activity. F. Self-organizing mechanisms in ant societies favor the emergence of behavioral castes that take care of brood. Photo by Ryan Hodnett, Wikimedia Commons.

Self-organized nest building

Almost all species of social insects build or dig a shelter shared by the colony [23]. Building a nest that can host the entire colony is a real challenge. In many cases, building is based on stigmergy with the emerging nest guiding and inducing the insects to perform additional work [16, 28]. For instance, during the construction of a termite mound (Fig. 1A), a termite depositing a clay pellet increases the probability that another termite will lay a pellet at the same location, thereby favoring the appearance of a pillar. At the same time, the formation of other pillars in the vicinity of the first one will be inhibited due to such factors as the local depletion of building material or the higher aggregation of termites around the

emerging pillar. Such a coupling of local activation with a distant inhibition will ultimately generate an orderly spacing of pillars.

Similarly, nest building in some social wasps is known to consist of a stimulus-response sequence in which the arrangement of nest cells serves as benchmark for the next stage of the construction process.

In these examples, the builders act directly on their environment, which in turn influences their behavior and/or that of their nestmates. Information from the work-in-progress coordinates the building activity of group members and ultimately leads to adaptive nest structures without any direct interaction among builders.

Self-organized foraging

Social insects are typically **central-place foragers** that bring resources back to the nest for shared use. The distribution of bees among flower patches is an example of a self-organized spatial pattern. Honey bee scouts transmit accurate spatial information through the **waggle dance**, which encodes both the distance and direction of a valuable flower patch [24]. Dance followers then fly out from the hive, use the acquired information to locate the patch and, in turn decide whether to advertise the patch by dancing. While each forager has a knowledge limited to its own particular flower patch, the colony as a whole can allocate bees according to the respective value of the different patches.

The network of foraging trails radiating out from an ant nest is another striking example of self-organized spatial structure [17]. Collective foraging on trails is a cooperative task based on the following sequence of interactions. When a scout has discovered a food source, she lays a trail that stimulates other ants to leave the nest and guides them to the food source. Once these recruited individuals reach the food, they can in turn reinforce the trail and thereby generate a positive feedback resulting in a non-linear increase of foragers at the food source. Furthermore, the reinforcement of the trail at some parts of the foraging space will concentrate workers at these locations and progressively channel the flow of foragers on a well-defined trail.

For both the honey bee and the ant colony, foraging dynamics are controlled by negative feedback such as the fading of an odor trail, colony satiation or the limited number of available recruits [12]. The intensity of recruitment will also automatically decrease when foragers become unable to feed due to food depletion or food overcrowding. Negative feedback is therefore based on the physicochemical properties of the exchanged signal (trail fading through evaporation) but also on the behavioral rules (no further reinforcement of the odor trail or no dance when unable to feed). Ultimately, the coupling of these positive and negative feedbacks allows the foraging dynamics and trail patterns to be adjusted to colony needs and resource availabilities.

Self-organized temporal patterns

Beside spatial patterns, temporal patterns also characterize insect societies that may display a high level of synchronicity in their activity. While many activities are regulated by a circadian pacemaker, a synchronicity of behaviors may emerge simply from interactions among the insects without being driven by an internal or external clock [8]. For instance, thousands of male fireflies gathered in the same trees can flash in synchronicity during

nocturnal mating displays. Each insect has his own rhythm, but the perception of his neighbors' lights brings that rhythm into synchrony with those around it. This synchronization emerges spontaneously without any external stimulus coordinating the flashing behavior.

Similarly, *Temnothorax allardycei* ant colonies may exhibit rhythmic changes in their activity levels with a 30-minute periodicity. Since isolated workers do not show such a periodicity, the large-scale synchronization of the entire colony results from the mutual activation of individuals with their neighbors. Thus, ants act as excitable units that spontaneously harmonize their level of activity by reciprocal influence of each other's rhythms [6].

Self-organization is also involved in the synchronization of the circadian rhythm of honey bee workers in the hive [2, 20]. Workers possess their own circadian rhythms that can be phase shifted when individuals are isolated. However, when reunited, out-of-phase workers can spontaneously uniformize their rhythm thanks to the intragroup variation of temperature that acts as a collective pacemaker. Such temporal synchronicity can be essential to the appearance of collective behaviors that requires a sufficient number of individuals to be simultaneously aroused and active.

Synchronicity is also observed in a defensive strategy against predatory wasps by Asian giant honey bees. The bees cover the surface of their nest, which consists of an exposed comb. When they detect a predator, the bees produce a synchronized repelling behavior by raising and lowering their abdomen. This behavior propagates from neighbor to neighbor forming organized waves at the surface of the comb that repulse the attacking wasps.

Self-organized collective choices

Several types of organization allow group members to reach a consensus. In some animal and human groups, the final decision can be made by only one individual who occupies a dominant position in the group, while in other groups decisions rely on all or at least a part of the group. Self-organized decision-making pertains to this last situation. In this, the probability of an individual evaluating a given option (e.g. a food source) increases with the number of conspecifics that have already selected that option. This creates a positive feedback as more and more individuals make the same choice.

Although such decentralized decision-making is based on individuals that each have access only to partial and local information, the colony as a whole can usually select the best of multiple options. Classical examples include the use of the shortest path between a food source and the nest ([15], Fig. 2), the collective selection of the richest food source [11], and the choice of the best nest site among those available [13, 25].

These examples raise the question of how the colony processes the information collected by different individuals and to what extent individuals with only limited information can influence the collective choice. It is usually impossible for an individual to directly sample, evaluate, and compare all available options. Likewise, informed individuals cannot contact all nestmates simultaneously, so that they usually only inform and recruit a small fraction of their colony. In ants, additional foragers are mobilized in small groups (ranging from one recruit in tandem-running species to a few individuals in group recruiting

species) by informed leaders, or by a chemical trail laid by the successful scout on her return to the nest. In honeybees, recruits are mobilized in the nest by the waggle dance performed by the recruiters that indicates the spatial location of a patch of flowers. Each forager can influence the final outcome by tuning the intensity of the recruitment signal to the quality of the food source. Towards high-quality resources, bee recruiters perform longer-lasting and more intense dances, while ants will deposit larger amount of trail pheromone. This biases the group's choice toward the most rewarding option without requiring any collective polling or direct comparison among available resources.

In this decentralized process, the first individuals that signal the presence of a resource may have a stronger impact on the group's ultimate choice. During the first stages of recruitment, recruiters with differing information will compete for the same pool of workers. Any small bias in favor of one option will be amplified and can finally monopolize the workforce. For this reason, self-organized choices can sometimes be suboptimal due to an amplification of a lower-quality discovery made by foragers early in the process. In this case, the colony can become committed to a poor option and unable to reverse its choice. Thus, self-organization appears to be an efficient way to share and process multiple sources of information in order to collectively choose the best of them, but it does not necessarily lead the colony to the best option.

Figure 2. Example of self-organized selection of the shortest path between the nest (N) and a food source (F). The first ant that discovers a food source comes back to the nest selecting branches at random and laying a chemical trail (A). Additional workers are recruited and start to exploit the food source. The trail along the shortest path becomes slightly more concentrated, mainly due to fewer detours (B). Thanks to the disproportionate probability of the ants to follow the most concentrated trail, the small bias in favor of the shortest path is

amplified to attract most of the workers (C). Figure by Nojhan, Wikimedia Commons, based on [20].

Self-organized division of labor

One of the main features of insect societies is division of labor, in which different members specialize (permanently or temporarily) in a subset of the colony-maintaining tasks [19]. Among the different existing models, the response-threshold model postulates that division of labor arises from variation among workers in their internal thresholds to external stimuli [4]. When the stimulus for a task exceeds a worker's threshold, the individual will perform that task. Task performance will then reduce the intensity of the stimulus, thereby reducing the likelihood that the task will be executed by other workers with higher thresholds. Furthermore, self-reinforcement processes may occur: performing a task will induce a decrease in the individual's corresponding threshold, while not performing it will increase the threshold [29]. This combined reinforcement will lead to the emergence of specialized workers. Accordingly, small initial individual variability in response thresholds may lead to large differences in task performance, with a division of labor appearing as an emergent property. The contribution of response thresholds to task organization has been experimentally demonstrated for several tasks, including wing fanning, removal of dead nestmates, and foraging in honey bees, as well as nest moving, brood care and foraging in ants.

Non-linearity in self-organized systems

In all examples presented above, one may usually find a sharp transition between two qualitative states of the colony, such as random to organized foraging, unsynchronized activities to a coordinated activity pattern, or the random deposit of building material to the emergence of a pillar. In addition, the insect colonies seem to transition discontinuously from one pattern to the other without showing intermediate levels of organization. These transitions are the result of the non-linear properties of the self-organized systems [7, 21, 27]. Non-linearity refers to the property of a system to react disproportionately to a perturbation. For example, if the foraging efficiency of a colony were linearly related to the number of foragers, the net gain in food retrieval obtained by adding 20 foragers should be twice as much as the gain from adding 10 foragers. However, if the net gain obtained by adding 20 foragers were substantially larger or substantially less than this, then foraging activity shows non-linear properties. In many examples of self-organized behavior, the whole society shows a non-linear response to an increase in the number of interactions at the individual level. For example, a critical group size is often required for the emergence of a collective trail, synchronicity of an activity, or aggregation under a common shelter. Because of this non-linearity, when a critical colony size, nestmate density or activity level is reached, any information about the environment (e.g. the location of food pellets) or small change in information-laden cues (e.g. a locally higher density of trail marks) can be amplified by interacting workers to lead to a macroscopic organization.

To illustrate these concepts, we present a case study of foraging in which three different strategies are used to collect food: (i) individual foraging, (ii) group recruitment, and (iii) trail recruitment. For the three "species", it is possible to develop mathematical models

describing the dynamics of food exploitation by the foragers, i.e. the number of workers present at the food source over time. In the three cases, the number of workers at the food source starts at zero, but once the food source is discovered it increases to a plateau value where it remains stationary. Again, thanks to modelling, one can predict the evolution of these stationary states as a function of different parameters, such as the number of workers, the intensity of the recruitment signal, or the duration of a foraging trip.

Figure 3. Dynamics of exploitation of a food source by colonies performing individual foraging (A), group recruitment (B), or trail recruitment (C). Evolution of the stationary states according to a key parameter of the recruitment and illustration of the expected behavior of a colony exploiting a food source (F) for two different values of this parameters: the spontaneous probability to exit the nest for individual foraging (D), the number of recruits contacted by the recruiters for group recruitment (E) and the quantity of pheromone laid by recruiters for trail recruitment (F). Green lines represent stable stationary states, red lines represent unstable stationary states.

In the case of individual foraging (A), each forager has a fixed probability of leaving the nest and having success in finding the resource. Over time, this results in a continuous mobilization of the workers to the feeder (Fig. 3A). The number of mobilized foragers will then stabilize at a plateau value that depends on the population size or time that each individual spends foraging. When keeping the above-mentioned parameters constant, the plateau value increases monotonically with the probability of each individual leaving the nest and finding the resource (Fig. 3D). As a result, more ants will be present at the food source if this probability is higher, even though there is no positive feedback in the foraging process; that is, one worker's search does not influence the behavior of others.

The second species (B) forages cooperatively through group recruitment. In this, each successful forager has a probability of contacting and recruiting a group of nestmates to the food source by physically guiding them (as observed in some ants) or by providing them with spatial information (as in honey bees). This initially results in low rate of nestmate recruitment. However, once a sufficient number of individuals participate in the recruitment, the number of foragers at the food source sharply increases until a plateau (Fig. 3b). The value of this plateau varies according to the number of nestmates mobilized per informed recruiter, all other parameters being fixed (Fig. 3E). Since some recruits will lose contact with the leader (ants) or will fail to accurately use spatial information to reach the flower patch (honey bees), a threshold recruited group size of recruits (at least three recruits in our example) is required for the population of available workers to collectively exploit the food source. Below this threshold value, the number of recruits that reach the food will be too small to generate a positive-feedback effect, and no collective exploitation of the food source will emerge. Furthermore, any increase of the group size that remains below the threshold will have very little effect on the number of mobilized foragers, with food not being collectively exploited. Likewise, as soon as the number of recruits per group is above the threshold value, any further increase (e.g. from 4 to 7) will result in only a small increase in the number of foragers exploiting the food. The social system thus exhibits an abrupt transition between two qualitatively distinct foraging patterns (null versus collective exploitation), this transition taking place for a critical value of recruited group size. In this case, the transition from one state to the other is achieved by passing the threshold value, independently of the direction of the transition, as there is only one transition point.

In our third example (C), recruitment is triggered by laying a trail pheromone, as observed in the majority of ant species. The trail will stimulate the exit of other nestmates and may generate trail patterns that guide them to the food source. As in group recruitment, the dynamics of trail recruitment are non-linear. The number of foragers at the food source slightly increases during the first steps of the recruitment. However, once a sufficient number of recruiters reinforce the chemical trail, the number of foragers sharply increases until it reaches a steady state. The plateau value of this steady state depends on the intensity of the recruiting signal, and this relationship takes the form of an “S”.

As shown on Fig. 3F, at low trail intensities colonies will be unable to collectively exploit food, while high intensities will draw a large number of ants at the food source. Interestingly, three possible steady states can exist for intermediate trail intensities (from 1 unit to 2 units in the example). Two of them are stable (green in Fig. 3F) and correspond to the absence or presence of a collective exploitation. The third steady state (red in Fig. 3F) is unstable, so that any small variation in the number of foragers will be amplified and will drive the colony towards a high or a low food exploitation. This non-trivial outcome can be experienced by behavioral ecologists, as some among a series of replicates of recruitment may not result in collective food exploitation for no apparent reason. Such seemingly failed recruitment may simply reflect multiple steady states in which a “null” and a “collective” exploitation are possible outcomes of the same amount of recruiting signal.

In this range of intermediate trail amounts, the observed steady state also depends on the history of the system. In a natural scenario, just after food discovery, the colony remains in a low-exploitation regime (the lower branch in Fig. 3) until the trail amount laid by the ants

exceeds a critical value (here $q = 2$) and draws the colony to abruptly transition to a high-exploitation regime (the upper branch in Fig. 3). However, once recruitment is well established, the society can remain in the high-exploitation regime even for trail amounts smaller than $q = 2$ and will return to a low-exploitation regime only if the quantity of pheromone falls below $q = 1$. This illustrates the concept of hysteresis in social behavior, in which the transition from one type of organization to another depends on the system's history. In the case of trail recruitment by ants, this means that, once recruitment is launched, foragers can reduce the amount of released pheromone without reducing the foraging efficiency at the colony level. Thus, the transition from a non-cooperative toward a collective behavior can be costly at first (e.g. in terms of signal emission), but the inertia of the self-organized behavior allows for cheaper maintenance as well as a more robust collective response to fluctuations of the environment.

Conclusion

In insect societies, each worker has limited cognitive abilities, assesses only local environmental parameters, and cannot compare its experience to that of all of its nestmates. Such individual limitations contrast with the diversity and complexity of collective responses that efficiently meet environmental opportunities and challenges. Self-organization allows insect societies to bridge the gap between these two levels of complexity. Due to the parsimony of the underlying mechanisms, self-organization appears to be the keystone on which a wide array of collective behaviors is built, such as nest building, foraging, activity rhythms, collective decision-making, and task partitioning. A macroscopic organization emerges from multiple local interactions between group members, which involve competing amplification processes and limiting factors. Social positive feedback usually depends on a critical density of interactions allowing the propagation of information-laden signals or activity to other nestmates. Overall, self-organization is a simple but powerful pattern-generating mechanism and therefore a powerful generator of biological diversity. This has made self-organization, among other coordinative mechanisms such as leadership or recipe, one of the most universal coordinative mechanisms across the animal kingdom.

References

1. Ball, P. – 1999. *The Self-Made Tapestry. Pattern Formation in Nature*. Oxford: Oxford University Press.
2. Block, G. – 2010. The Social Clock of the Honeybee. *Journal of Biological Rhythms*, 25:307-317.
3. Bonabeau, E., Theraulaz, G., Deneubourg, J.L., Aron, S. & Camazine, S. – 1997. Self-organization in social insects. *Trends in Ecology & Evolution*, 12:188-193.
4. Bonabeau, E., Theraulaz, G. & Deneubourg, J.L. – 1998. Fixed Response Thresholds and the Regulation of Division of Labor in Insect Societies. *Bulletin of Mathematical Biology*, 60:753-807.
5. Camazine, S., Deneubourg, J.L., Franks, N.R., Sneyd, J., Theraulaz, G. & Bonabeau, E. – 2001 *Self-organization in biological systems*. Princeton: Princeton University Press.

6. Cole, B.J. – 1991. Short-term activity cycles in ants: generation of periodicity by worker interaction. *American Naturalist*, 137:244-259.
7. Collignon, B., Deneubourg, J.L. & Detrain, C. – 2012. Leader-based and self-organized communication: modelling group-mass recruitment in ants. *Journal of Theoretical Biology*, 313:79-86.
8. Couzin, I.D. – 2018. Synchronization: The Key to Effective Communication in Animal Collectives. *Trends in Cognitive Sciences*, 22:844-846.
9. Couzin, I.D. & Krause, J. – 2003. Self-Organization and Collective Behavior in Vertebrates. *Advances in the Study of Behavior*, 32:1-75.
10. Deneubourg, J.L. & Goss, S. – 1989. Collective patterns and decision-making. *Ethology, Ecology & Evolution*, 1:295-311.
11. Detrain, C. & Deneubourg, J.L. – 2006. Self-organized structures in a superorganism: do ants ‘behave’ like molecules? *Physics of Life Reviews* 3, 162–187.
12. Detrain, C. & Deneubourg, J.L. – 2008. Collective decision-making and foraging patterns in ants and honeybees. *Advances in Insect Physiology*, 35:123-173.
13. Franks, N.R., Pratt, S.C., Mallon, E.B., Britton, N.F. & Sumpter, D.J.T. – 2002. Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences*, 357:1567-1583.
14. Gordon, D.M. – 2010. Ant Encounters. Interaction Network and Colony Behavior. Princeton University Press, Princeton.
15. Goss, S., Aron, S., Deneubourg, J.-L., & Pasteels, J. (1989). Self-organized short-cuts in the Argentine ant. *Naturwissenschaften*, 76, 579-581.
16. Grassé, P.P. – 1959. La reconstruction du nid et les coordinations interindividuelles chez *Bellicositermes natalensis* et *Cubitermes* sp. La théorie de la stigmergie : essai d’interprétation du comportement des termites constructeurs. *Insectes Sociaux*, 6:41-81.
17. Hölldobler, B. & Wilson, E.O. – 1990. The Ants. Berlin: Springer.
18. Jeanson, R., Dussutour, A. & Fourcassié, V. – 2012 Key factors for the emergence of collective decision in invertebrates. *Frontiers in Neuroscience*, 6:121.
19. Jeanson, R. & Weidenmüller, A. – 2014. Interindividual variability in social insects – proximate causes and ultimate consequences. *Biological Reviews*, 89:671-687.
20. Moritz, R.F.A. & Kryger, P. – 1994. Self-organization of circadian rhythms in groups of honeybees (*Apis mellifera* L.). *Behavioral Ecology & Sociobiology*, 34:211-215.
21. Nicolis, S. & Deneubourg, J.L. – 1999. Emerging Patterns and Food Recruitment in Ants: an Analytical Study. *Journal of Theoretical Biology*, 198:575-592.
22. Nicolis, G. & Prigogine, I. – 1977. Self-organization in nonequilibrium systems. New York:Wiley.
23. Perna, A. & Theraulaz, G. – 2017. When social behaviour is moulded in clay: on growth and form of social insect nest. *Journal of Experimental Biology*, 220:83-91.
24. Seeley, T.D. – 1995. The Wisdom of the Hive. Cambridge: Harvard University Press.
25. Seeley, T.D. & Buhrman, S.C. – 1999. Group decision making in swarms of honey bees. *Behavioral Ecology & Sociobiology*, 45:19-31.

- 459 26. Sumpter, D.J.T. – 2010. *Collective Animal Behavior*. Princeton: Princeton University
460 Press.
- 461 27. Sumpter, D.J.T. & Beekman, M. – 2003. From nonlinearity to optimality: pheromone
462 trail foraging by ants. *Animal Behaviour*, 66:273-280.
- 463 28. Theraulaz, G., Bonabeau, E. & Deneubourg, J.. – 1998. The origin of nest complexity
464 in social insects. *Journal of Complexity*, 3:15-25.
- 465 29. Weidmüller, A. – 2004. The control of nest climate in bumblebee (*Bombus*
466 *terrestris*) colonies: interindividual variability and self reinforcement in fanning
467 response. *Behavioral Ecology*, 15:120-128.