Reference: *Biol. Bull.* **202:** 262–267. (June 2002)

Dynamics of Aggregation and Emergence of Cooperation

J. L. DENEUBOURG*, A. LIONI, AND C. DETRAIN

Université Libre de Bruxelles, Unit of Social Ecology, CP 231. B-1050 Brussels, Belgium

Abstract. Aggregation is one of the most basic social phenomena, and many activities of social insects are linked to it. For instance, the selection of a valuable site and the spatial organization of the population are very often by-products of amplifications based on the local density of nestmates. The patterns of aggregation are very diverse, ranging from the gathering of all animals in a unique site to their splitting between several ones. One might question how these multiple patterns emerge. Do ants actively initiate the formation of such patterns by modulating the emission of an attracting signal such as the trail pheromone? Alternatively, do patterns result from quantitative changes in the duration of interaction between animals once they have reached the gathering site, without any active modulation of the communications? To discuss these questions, we present two empirical studies: the gregarious behavior of cockroaches (*Blatella*) and self-assembly in the weaver ant (*Oecophylla*).

Through experimental and theoretical studies, we show how a single behavior—the resting time—leads to a collective choice in both species. This behavior is a response to the density of conspecifics and can also be modulated by heterogeneities in the environment. In weaver ants, it allows the colony to focus the formation of chains in a given area among several potential sites. In cockroaches, it allows the gathering of individuals in particular shelters, depending on the proximity between strains. These results are discussed with emphasis on the role of aggregation processes in the emergence of cooperativity and task allocation.

* To whom correspondence should be addressed. E-mail: jldeneub@ulb.ac.be

This paper was originally presented at a workshop titled *The Limits to Self-Organization in Biological Systems*. The workshop, which was held at the J. Erik Jonsson Center of the National Academy of Sciences, Woods Hole, Massachusetts, from 11–13 May 2001, was sponsored by the Center for Advanced Studies in the Space Life Sciences at the Marine Biological Laboratory, and funded by the National Aeronautics and Space Administration under Cooperative Agreement NCC 2-896.

Introduction

In animal societies, collective decisions and patterns emerge from a variety of interactions among individuals. Self-organization is the theory of how minimal complexity at the individual level can generate much greater complexity at the collective one. The rules specifying the interactions among the system's components are executed using only local information, that is, without reference to the global pattern. Thus collective decisions that can be made using rules of thumb that require only a limited cognitive ability and a limited knowledge of the environment might be characterized in terms of the multiplicity of parameters as well as by heterogeneity and unpredictability (Camazine *et al.*, 2001).

Most self-organized decisions and patterns arise as a result of a competition between different sources of information that are then amplified through different forms of positive feedback. In contrast, negative feedback often arises "automatically" as a result of the system's constraints (*e.g.*, limits on the supply of food, the space for settlement, and the number of available workers). An example of such processes is the competition between trail recruitments to multiple food sources in social insects or gregarious arthropods (social caterpillars or spiders) where the modulation of communication is essential (Deneubourg and Goss, 1989; Camazine *et al.*, 1990, 2001; Camazine and Sneyd, 1991; Seeley *et al.*, 1991; Seeley, 1995; Fitzgerald, 1995; Detrain *et al.*, 1999; Saffre *et al.*, 1999). For instance, the ability of a bee or an ant to modulate its dancing or trail-laying behaviors, in relation to its perception of the profitability of a particular source, is sufficient for a collective and adapted decision to be made.

We generally observe a high diversity of collective patterns at both intraspecific and interspecific levels. But how is this diversity produced in self-organized systems? Do individuals need specific behavioral algorithms and a modulation of their communication for each situation? Or do

they just modulate some generic rules without changing their individual interactions? Can we find a convergence of similar and simple mechanisms for different species and for different collective tasks? These are fundamental questions, not only for better understanding mechanisms of organization, but also for making the link between the proximal and ultimate view of social evolution (Krebs and Davies, 1997).

To discuss these questions, we choose to focus on a very widespread phenomenon, that of aggregation. It is of particular interest because it is a prerequisite for the development of other forms of cooperation and is involved in many tasks performed by an insect society. In addition, the gathering of individuals at the same place is significant because it is often the consequence of a collective choice.

Through two empirical studies—on the gregarious behavior of cockroaches (*Blattela germanica*) and on self-assembly in weaver ants (*Oecophylla*)—we show (1) how collective decisions are a by-product of the mechanisms involved in aggregation; and (2) how different collective patterns, with different functions, arise from the same generic rules, based on the individual response (mainly the resting time) to local signals including the presence of conspecifics (positive feedback). Though we do not deny the possible modulation of a signal depending on the environment, we demonstrate here that such modulation is neither observed nor necessary for the emergence of aggregation patterns.

Self-Assembly in *Oecophylla*

Ants of the genus *Oecophylla* (Ledoux, 1950; Hölldobler and Wilson, 1978, 1990; Lioni *et al.*, 2001; Lioni and Deneubourg, unpubl. data) are characterized by their capacity to hang on to each other to form chains. This allows the bridging of an empty space, for example between two branches (see Hölldobler and Wilson, 1990, pp. 618–629). These self-assembled structures are a particular type of aggregation. In nature the challenge of such an activity is to avoid the formation of multiple small and inefficient chains. What are the mechanisms that allow the colony to focus its activity at a particular and useful site?

To address this question, we set up an experimental apparatus using a binary choice (Fig. 1a), and we observed how the probability of an ant entering (P_{ei}) or leaving (P_{li}) a chain depends on the size of the chain (Fig. 1b). We found that

$$P_{ei} = a + \frac{bX_i}{1 + cX_i} \quad (1)$$

$$P_{li} = \frac{dX_i}{1 + eX_i^h} \quad (2)$$

where X_i is the number of ants in the chain i.

The fitting of the experimental values gives the following parameter values: $a = 0.55$; $b = 0.11$; $c = 0.28$ ($r = 0.89$; $P < 0.001$); $d = 0.33$; $e = 0.48$; $h = 1.3$ ($r = 0.92$; $P < 0.001$).

The function P_{ei} expresses the idea that the probability for an ant to join the chain grows with the number of nestmates already present (X) and reaches a plateau value equal to $a + bX_i$; a is the value of spontaneous hanging when $X_i = 0$. The probability for an ant to leave the chain (P_{li}) decreases with X_i. Considering T_p as the total population in the nest, we also observed a linear dependence between the arrival flow ϕ_p and the population remaining in the nest ($T_p - (X_1 + X_2)$).

At the beginning of the experiment, we observe a similar increase in the number of ants in both chains. A slight asymmetry between the populations appears, after 10 min, and is amplified during the rest of the experiments. After 20 min there is a strong asymmetry, which results in the survival of one chain with a high number of ants (Fig. 2). The asymmetry is not due to a higher flow of arrivals from the nest to the strongest chain (this flow remains equal on both branches); it is due only to the process of the ants entering and leaving the chains.

Positive feedback mechanisms expressed by equations (1) and (2) generate a nonlinear growth that focuses activity on a single and functional chain instead of on several small and inefficient ones.

Furthermore, these probabilities (P_{ei}) and (P_{li}) can be triggered by the presence of a visual stimulus or by the geometry of the environment (*e.g.*, a dead-end). The symmetry of the set-up can be broken by placing a visual stimulus under one branch (black bar, 1 cm width, placed 6 cm below one branch). In this situation the growth and the persistence of the chain above the stimulus are favored (Fig. 3). There is still an equal flow of arrivals on both branches, and the same logic applies as in the symmetrical setup. The visual stimulus quantitatively changes the individual response by slightly increasing P_e and decreasing P_1, thereby increasing the resting time in the chain. As a result, the visual stimulus can be reached by the ants, and the chain is used as a bridge.

To summarize, this example shows that a slight modulation of the resting time, which corresponds to $1/P_1$, can generate different patterns and allow the colony to focus its activity. The individual response is based on the local density of nestmates and can be triggered by any favorable configuration, such as the presence of leaves in a tree. It is important to note that this decision is reached without any need for an active modulation of the communication.

Cockroach Aggregation and Strain Odor Recognition

Cockroaches in the species *Blattella germanica* exhibit gregarious behavior in shelters during their resting period. The shelters are an important resource for these insects, and the gregarious behavior facilitates cooperation (Dambach and Goehlen, 1999). Binary choice tests were carried out

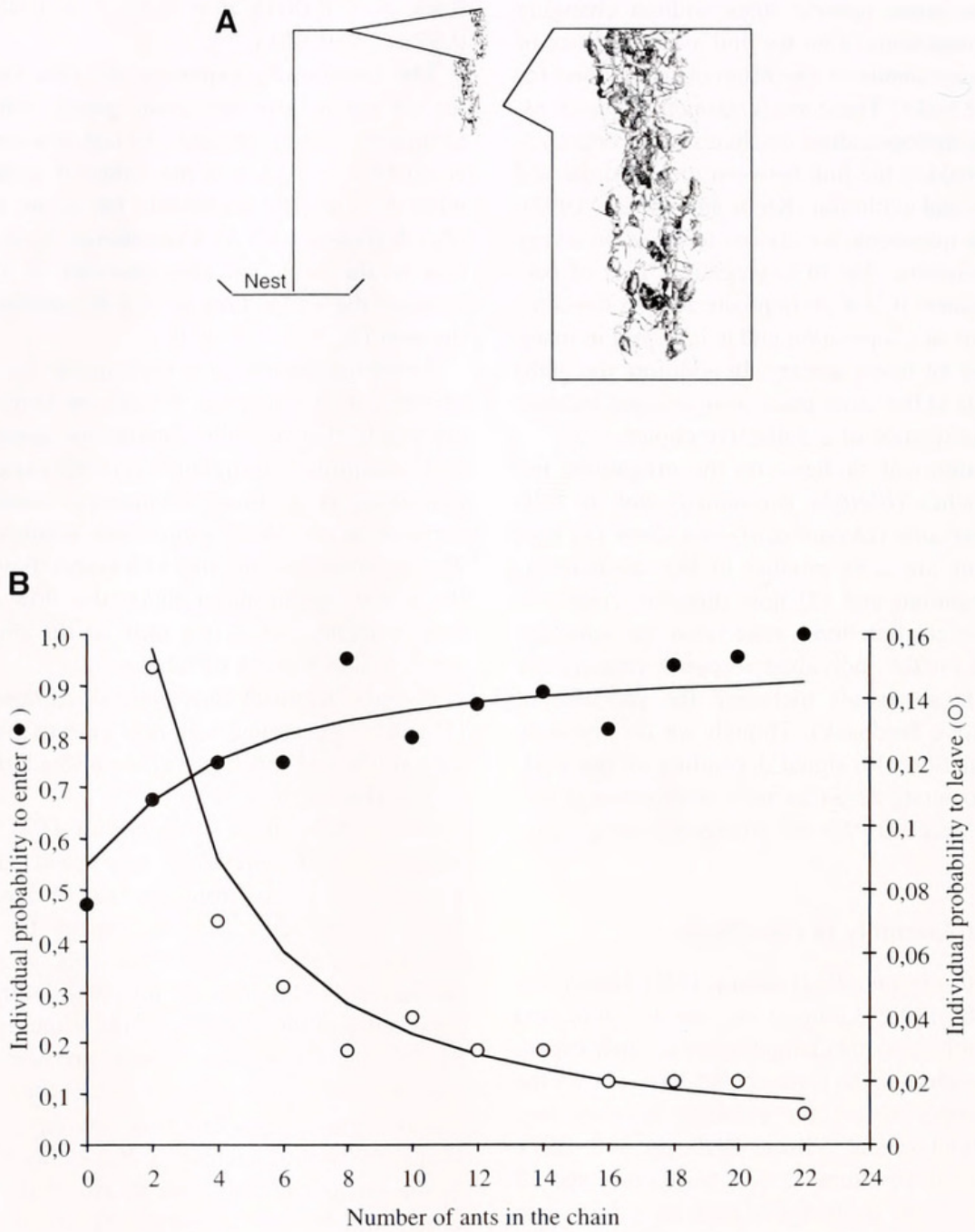

Figure 1. (A) Binary choice experimental set-up used to study chain competition in weaver ants. (B) Individual probabilities to enter a chain depending on its size (●) and to leave a chain depending on its size (○).

between two large and identical shelters each with a carrying capacity (S) large enough to contain the whole population. Tested groups of larvae show a strong tendency to aggregate on a unique, randomly selected, resting site (Fig. 4; Rivault and Cloarec, 1998). This collective choice results from a random walk and hence random discovery of the shelter by larvae and a probability P_i to leave the shelter i (P_i = 1/resting time). Due to inter-attraction between individuals, this probability decreases with the number of conspecifics (X_i) in the shelter i and is ruled by an empirical equation very similar to that proposed for *Oecophylla* (Rivault *et al.*, 1999; Ame *et al.*, Université Libre de Bruxelles, unpubl. data):

$$P_i = \frac{a}{1 + bX_i^2} \tag{3}$$

with $a = 0.01$, $b = 0.16$. The characteristics of the shelter affect the resting time of the individuals, which for an isolated animal is $\cong 1/a$. The expression $(1 + bX_i^2)$ describes how the presence of other conspecifics increase the resting time. A theoretical model suggests that these basic mechanisms account for the clustering of insects (Rivault *et al.*, 1999; Ame *et al.*, unpubl. data). This model also predicts that other collective patterns can emerge, keeping the same individual rules.

For instance, a group of cockroaches is able to select a

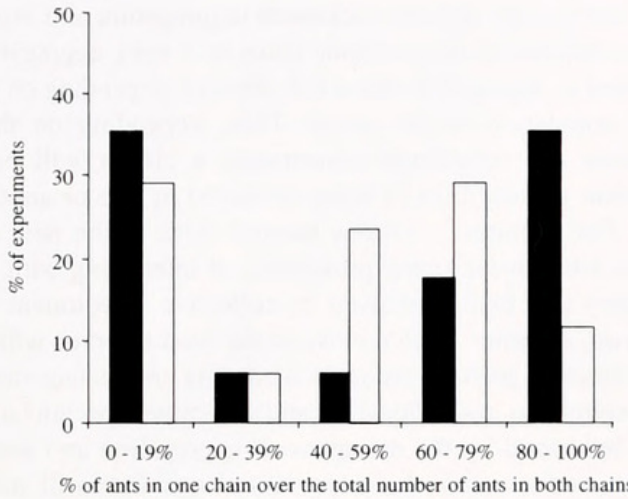

Figure 2. Distributions of the proportion of ants in one chain on the total number of ants in each chain at times 2 (□) and 20 min (■) ($N = 19$).

single shelter only if the number of shelters is small or its population is large. This result shows that different patterns of aggregation may be spontaneously adopted based only on changes in the environment.

In natural situations, the shelters are not identical, and they are characterized by different parameters, which are more or less easily detected and integrated by an individual. Any parameter of the shelter that increases the individual resting time favors the formation of the cluster in this shelter. Because of the competition between shelters, most of the larvae will aggregate in the site that has the highest resting time. Furthermore, the interactions between individuals increase the probability of an individual staying on the site that produces the largest resting time and benefit *per capita*.

Individual tests show that the larvae prefer the odor of their own strain to that of another (Rivault *et al.*, 1999). However, in mixed groups with individuals from two strains, experiments show that the final aggregation is not different for mixed or pure groups (Rivault and Cloarec, 1998). In simulations, it is rather easy to take these interactions between strains into account:

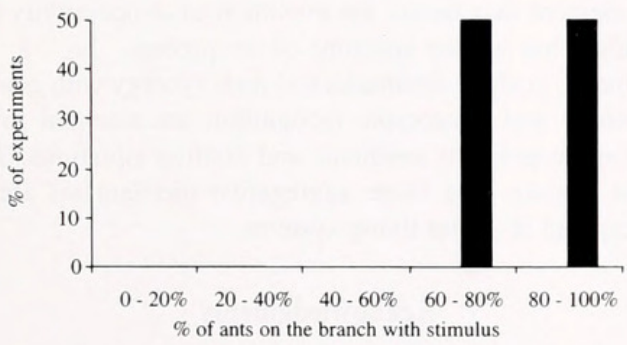

Figure 3. Distributions of the proportion of ants in the chain above the stimulus, on the total number of ants in each chain at 10 min ($N = 6$).

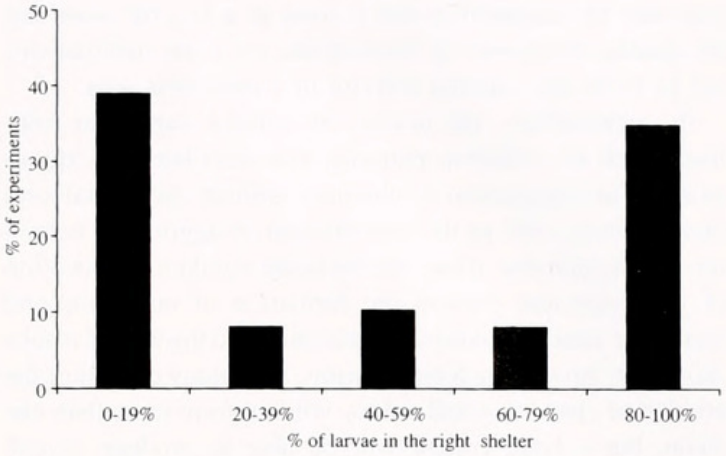

Figure 4. Experimental distribution of the proportion of cockroach larvae present in shelter 1 ($n = 49$). Number of larvae in each tested group = 20.

$$P_{1i} = \frac{a}{1 + b(X_{1i} + \beta X_{2i})^2} \tag{4}$$

$$P_{2i} = \frac{a}{1 + b(X_{2i} + \beta X_{1i})^2} \tag{5}$$

where P_1 (P_2) are the probabilities for an individual of strain 1 (2) to leave the shelter i, X_{1i} and X_{2i} are respectively the number of individuals of strain 1 and 2 in this shelter i. β is the inter-attraction between both strains: if $\beta = 1$, there is no difference between the strains; and if $\beta = 0$, there is no inter-attraction between the strains. Simulations show that even with a very low attractivity between strains (β is low), there is no difference between the gregarious patterns of mixed and pure groups.

However, the model also predicts that the two strains are able to segregate when the resting sites are overcrowded ($S \cong$ total population). Each cluster is characterized by a majority of larvae from the same strain. In this case, group closure is an emergent component of the dynamics, in that the segregation is obtained without aggressive parameters or any other form of repulsion between strains. The smaller the shelter and the greater the difference between the two strains (β small), the more easily the segregation emerges. If the two strains are similar enough ($\beta > 0.5$), the segregation is never observed. To summarize, the crowding in the shelter and the degree to which individuals recognize each other (proximity between strains given by β) affect the dynamics of aggregation and lead to opposite patterns.

Conclusion and Perspectives

Both examples given in this paper illustrate how one parameter (here the resting time) can produce different patterns of aggregation independent of any active signaling by animals. In cockroaches, the amplification is modulated only by the time spent in a shelter, which is enough to produce the patterns. The resting time is increased by the

presence of conspecifics and is used as a key for assessing the quality of the site. In *Oecophylla,* the same mechanisms act to focus the colonial activity in a particular area.

In cockroaches, the unique modulated parameter contrasts with the different patterns. The shift between aggregation and segregation is obtained without any behavioral modification, such as the introduction of aggressive behavior. In *Oecophylla,* these mechanisms regulate the location of the chain and prevent the formation of numerous and inefficient ones. Moreover, experimental and theoretical results show that, through such mechanisms, the colony can adjust the number of chains: a small colony will not form more than one chain, but a large colony will be able to produce several functional chains (Lioni and Deneubourg, unpubl. data).

Our conviction is that these self-organized processes are numerous despite the fact that the individual or group benefits will differ and will occur in different situations. The mechanisms involved in the aggregation and segregation of the cockroaches—amplification of the resting time and chemical recognition—could have their equivalent in different spatial organization of items by insect societies (Camazine, 1991; Deneubourg *et al.,* 1991; Franks and Sendova-Franks, 1992) and of workers from different castes or from different matrilines or patrilines. For gregarious and eusocial insects, communication relies essentially on chemical signals and amplification mechanisms (Camazine *et al.,* 2001). Phenotypic recognition that is mainly chemically based (Vander Meer and Morel, 1998; Rivault *et al.,* 1998, 1999; Lenoir *et al.,* 1999) can be modulated by genetic background and environment and can be associated with division of labor (Bonavita-Cougourdan and Clement, 1994; Wagner *et al.,* 1998).

In the context of self-organization and transition between different social organizations, aggregation, and its resulting increase in density, is a prerequisite for the emergence of higher forms of cooperation. The density could be involved in, or even lead, the process of the social differentiation. The interplay between amplification mechanisms (*e.g.,* growth or learning) and the competition in a cluster could be enough to produce the social differentiation that has been described for very different species, such as social spiders (Rypstra, 1993), sea urchins (Grosjean *et al.,* 1996), and ant queens (Fewell and Page, 1999); for a model, see Bonabeau *et al.* (1998).

Considering specifically the eusocial species, one of the key questions is the emergence of division of labor. Though there is no doubt that some genetic or physiological aspects must be taken into account (Page and Erber, 2002), we can assume that division of labor is also the result of self-organized mechanisms where amplification is essential (Beshers and Fewell, 2001). Eusocieties express a strong correlation between the colony size and the level of individual specialization (Anderson and McShea, 2001): the bigger the colony, the higher the specialization. As we have shown in the weaver ant (the number of chains depends on the colony size) and the cockroach (aggregation and segregation depend on the available place on a site), aggregation can lead to segregation into a few clusters, depending on the total population of the group. Thus, depending on their location, the individuals constituting a cluster will have different probabilities of being involved in one or another task. For example, a cluster located close to the nest entrance will have a higher probability of interacting with the foragers and being involved in collective recruitment. In contrast, a cluster located close to the food reserves will be stimulated to perform the tasks of sorting and management. To summarize, task allocation and individual specialization will be shaped by the dynamics of aggregation and segregation, and in return these specialized activities will shape the spatial organization within the nest.

The consequence of such a generic logic could then be one of the keys to understanding the transition between different forms of cooperativity, and therefore different degrees of sociality. For instance, it could help to explain how animal species have shifted, through evolution, from solitary to some simple forms of social life. Furthermore, it also brings new ideas on how a solitary species might be manipulated to become gregarious, or how a gregarious species might be manipulated to exhibit more complex forms of cooperation and social specialization (see, *e.g.,* the experimental shift from solitary to social organization in the spider *Coelotes terrestris,* Gunderman *et al.,* 1993). In this context, it is important to notice that even solitary species use amplification mechanisms based on the chemical marking of resting sites or on trail orientation (see, *e.g.,* for spiders, Saffre *et al.,* 1997; B. Krafft, Université de Nancy, pers. comm.).

Our theoretical results on cockroaches show that a slight inter-attraction between the marking of different individuals may induce the formation of a cluster (see also Saffre *et al.,* 1999). We could hypothesize that, for some species, this marking gives the opportunity to shift from solitary to gregarious behavior: the greater this phenotypic recognition, the easier the shift towards gregariousness. Because genetic proximity is one way to increase phenotypic recognition, the clustering of individuals having a similar genotype should be easier, and the synergy between amplification and genetic proximity should facilitate the emergence of cooperation. Therefore, we consider haplodiploidy to be one element that favors the evolution of cooperativity and sociality, but not the keystone of the process.

Finally, positive feedbacks and their synergy with genetic proximity and phenotypic recognition are essential to resolving cooperation problems and conflict situations. This could explain why these aggregative mechanisms are so widespread in group living systems.

Acknowledgments

Many thanks to J. M. Amé, Ph. Rasse, and C. Rivault (University of Rennes) for their interest and work on this

topics. Jean-Louis Deneubourg and Claire Detrain are research associates of the Belgian National Foundation for Scientific Research. This work was financially supported by grant number 2.4510.01 for Joint Basic Research. Jean-Louis Deneubourg thanks Les Instituts Solvay and the Santa Fe Institute, and the members of the working group "Social Insects."

Literature Cited

Anderson, C., and D. W. McShea. 2001. Individual versus social complexity. *Biol. Rev. (Camb.)* **76:** 211–237.

Beshers, S. N., and J. H. Fewell. 2001. Models of division of labor in social insects. *Annu. Rev. Entomol.* **46:** 413–440.

Bonabeau, E., J.-L. Deneubourg, and G. Theraulaz. 1998. Within brood competition and the optimal partitioning of parental investment. *Am. Nat.* **152:** 419–427.

Bonavita-Cougourdan, A., and J. L. Clement. 1994. Complexité du message chimique cuticulaire chez les fourmis: le modèle *Camponotus vagus* (Scop.) (Hymenoptera, Formicidae). *Memorabilia Zool.* **48:** 23–37.

Camazine, S. 1991. Self-organizing pattern formation on the combs of honey bee colonies. *Behav. Ecol. Sociobiol.* **28:** 61–76.

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

Camazine, S., J. Sneyd, M. J. Jenkins, and J. D. Murray. 1990. A mathematical model of self-organized pattern formation on the combs of honeybee colonies. *J. Theor. Biol.* **147:** 553–571.

Camazine, S., J. L. Deneubourg, N. Franks, J. Sneyd, E. Bonabeau, and G. Theraulaz. 2001. *Self-Organization in Biological Systems.* Princeton University Press, Princeton, NJ.

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

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

Deneubourg, J. L., S. Goss, N. Franks, A. Sendova-Franks, C. Detrain, and L. Chrétien. 1991. The dynamics of collective sorting: robot-like ants and ant-like robots. Pp. 356–365 in *From Animals to Animals: Proceedings of the First International Conference on Simulation of Adaptive Behavior,* J.-A. Meyer and S. Wilson, eds. MIT Press, Cambridge, MA.

Detrain, C., J. L. Deneubourg, and J. M. Pasteels. 1999. Decision-making in foraging by social insects. Pp. 331–354 in *Information Processing in Social Insects,* C. Detrain, J. L. Deneubourg, and J. M. Pasteels, eds. Birkhauser, Basel.

Fewell, J. H., and R. E. Page, Jr. 1999. The emergence of division of labour in forced associations of normally solitary ant queens. *Evol. Ecol. Res.* **1:** 537–548.

Fitzgerald, T. D. 1995. *The Tent Caterpillars.* Cornell University Press, Ithaca, NY.

Franks, N. R., and A. B. Sendova-Franks. 1992. Brood sorting by ants: distributing the workload over the work-surface. *Behav. Ecol. Sociobiol.* **30:** 109–123.

Grosjean, Ph., Ch. Spirlet, and M. Jangoux. 1996. Experimental study of growth in the echinoid *Paracentrotus lividus* (Lamarck, 1816) (Echinodermata). *J. Exp. Mar. Biol. Ecol.* **201:** 173–184.

Gunderman, J. L., A. Horel, and B. Krafft. 1993. Experimental manipulations of social tendencies in the subsocial spider *Coelotes terrestris. Insectes Soc.* **40:** 229–239.

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

Hölldobler, B., and E. O. Wilson. 1990. *The Ants.* Harvard University Press, Cambridge, MA.

Krebs, J. R., and N. B. Davies. 1997. *Behavioural Ecology: An Evolutionary Approach.* Blackwell Scientific, Oxford.

Ledoux, A. 1950. Recherche sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Ann. Sci. Nat. Zool.* Hème série, **13:** 313–409.

Lenoir A., D. Fresneau, C. Errard, and A. Hefetz. 1999. Individual and colonial identity in ants: the emergence of the social representation concept. Pp. 219–237 in *Information Processing in Social Insects,* C. Detrain, J. L. Deneubourg and J. M. Pasteels, eds. Birkhauser, Basel.

Lioni, A., C. Sauwens, G. Theraulaz, and J. L. Deneubourg. 2001. Chain formation in *Oecophylla longinoda. J. Insect Behav.* **15:** 679–696.

Page R. E., and J. Erber. 2002. Levels of behavioral organization and level of division of labour. *Naturwissenschaften* **89:** 91–106.

Rivault, C., and A. Cloarec. 1998. Cockroach aggregation: discrimination between strain odours in *Blattella germanica* (L). *Anim. Behav.* **55:** 177–184.

Rivault, C., A. Cloarec, and L. Streng. 1998. Cuticular extracts inducing aggregation in the German cockroach, *Blattela germanica* (L). *J. Insect Physiol.* **44:** 909–918.

Rivault, C., G. Theraulaz, A. Cloarec, and J. L. Deneubourg. 1999. Auto-organisation et reconnaissance coloniale: le modèle de l'agrégation de la blatte. Pp. 11–18 in *Actes Colloque Insectes Sociaux,* Vol. 12, J. P. Lachaud and V. Fourcassie, eds. L'Union Internationale pour l'Etude des Insectes Sociaux, Section Francaise, Paris.

Rypstra, A. L. 1993. Prey size, social competition, and the development of reproductive division of labor in social spider groups. *Am. Nat.* **142:** 868–880.

Saffre, F., B. Krafft, and J. L. Deneubourg. 1997. What are the mechanisms involved in the emergence of cooperativity? The "spider" model. Pp. 85–90 in *Auto-organisation et Comportement,* G. Theraulaz and F. Spitz, eds. Hermès, Paris.

Saffre, F., R. Furey, B. Krafft, and J. L. Deneubourg. 1999. Collective decision-making in social spiders: dragline-mediated amplification process acts as a recruitment mechanism. *J. Theor. Biol.* **198:** 507–517.

Seeley, T. D. 1995. *The Wisdom of the Hive.* Harvard University Press, Cambridge, MA.

Seeley, T. D., S. Camazine, and J. Sneyd. 1991. Collective decision-making in honey bees: how colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* **28:** 277–290.

Vander Meer, R. K., and L. Morel. 1998. Nestmate recognition in ants. Pp. 79–103 in *Pheromone Communication in Social Insects: Ants, Wasps, Bees and Termites,* R. K. Vander Meer and K. E. Espelie, eds. Westview Press, Boulder, CO.

Wagner, D., M. J. F. Brown, P. Broun, W. Cuevas, L. E. Moses, D. L. Chao, and D. M. Gordon. 1998. Task-related differences in the cuticular hydrocarbon composition of harvester ants, *Pogonomyrmex barbatus. J. Chem. Ecol.* **24:** 2021–2037.