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(Self-) Organized Activity

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At the suggestion of Professor Rüdiger Wehner, a Permanent Fellow of the Wissenschaftskolleg, four of us — Jean Louis Deneubourg, Nigel Franks, Tom Seeley and myself — were invited here in 1993 for a *Schwerpunkt.* Our group originally had the ungainly name "Self-Organizing Superorganism Systems (Collective Intelligence)." However, after our arrival we tried to shorten the title to "Self-Organizing Systems" which was both more appropriate for our topic of study and also had the advantage of avoiding the highly-charged term "intelligence" among the intellectuals of the Wissenschaftskolleg. Unfortunately, we did not succeed, and our fellow Fellows persisted in referring to us either as the "Collective Intelligence" group or the "Collective Unintelligence" group, depending upon their interpretation of our progress and their personal sympathies for us as individuals !

Our primary goal for the year was to work on a book' about self-organization in biological systems. I also hoped to develop a series of computer simulations to accompany the book. The environment of the Wissen-

[1] Camazine, S., Deneubourg, J. L., Franks, N., Seeley, T. *Building Biological Superstructures: Models of Self-Organization* (in preparation). See also pp. 255 ff. in this volume.

schaftskolleg has been an ideal setting for this work. The library facilities gave us ready access to the necessary literature, and the daily interaction with other members in the group provided a unique opportunity to develop ideas about the emerging field of self-organization.

What is self-organization? Self-organization is not a simple term to define. In general, it refers to the various mechanisms by which order and structure spontaneously emerge in complex systems. Examples of such structures and patterns include the stripes of zebras, the pattern of sand ripples in a dune, the coordinated movements of flocks of birds or schools of fish, the intricate earthen nests of termites, the whorls of our fingerprints and even the spatial pattern of stars in a spiral galaxy.

Our group at the Wissenschaftskolleg chose to focus the attention on a small subset of this universe of self-organized structures. We were interested primarily in biological systems involving groups of multicellular organisms, in particular the complex and intriguing insect societies of bees, ants and termites. In this context, self-organization is a process in which pattern emerges at the global (collective) level by means of interactions among components of the system at the individual level. What makes a system self-organized is that the collective patterns and structures arise without the guidance of well-informed leaders and without any set of predetermined blueprints, recipes or templates to explicitly specify the pattern. Instead, structure is an emergent property of the dynamic interactions among components in the system.

My own research may help clarify what we mean by self-organization. My work has been devoted to the study of honey bee societies. My goals have been to explore the remarkable social organization of insect societies and to unravel the mechanisms produced by natural selection that enable these societies to function as coherent, well-organized entities. A colony of insects faces the same challenges confronting an individual organism — defense, the need for nourishment, and reproduction. But though a colony may be a well-integrated unit, it nonetheless consists of many separate individuals, each relatively autonomous, and each relatively simple. Whereas the cells that constitute an individual organism are interconnected by extensive neural and circulatory networks, the members of a colony are only loosely connected. This raises the question of how the colony accomplishes its remarkable collective feats. How are colony-level decisions made without the colony equivalent of a brain or an organizing committee? How is colony homeostasis maintained without a sophisticated information network to relay data to a central control unit? Towards this end, my approach has been to view the insect society as a complex system of interacting units, and to examine how collective phenomena emerge from simple interactions among individual colony members. This approach couples extensive experimental observations with mathematical modelling and computer simulation. I have recently been working on the following topics: (1) the regulation of pollen foraging, (2) the formation of the concentric pattern of brood, pollen and honey on the comb, (3) the thermoregulation of colonies in winter, and (4) the social organization of the defensive behavior in European and Africanized honey bees.

How do the foragers of a honey bee colony know how much pollen to collect in order to feed the colony members? This is an example of collective activity that is precisely organized and carefully regulated. However, we know very little about the actual mechanisms that regulate pollen collection. Working with marked bees in observation hives, I have begun to unravel some of the mysteries of pollen foraging. I have shown that the colony experiences wide, rapid fluctuations in pollen stores and that the individual bees quickly respond to these changes by varying their rate of pollen collection. My current focus is to determine the precise cues by which the individual foragers assess their colony's need for pollen. Although we are still far from a complete understanding of the process, some valuable progress has been made.

When the colony is subjected to low pollen reserves, more bees forage for pollen, and each individual forages more rapidly. Conversely, if the colonies are given excess pollen, the foragers slow down their foraging rate or cease to forage. The homeostatic response by the foragers develops within a few hours of changes in the colony's pollen reserves, yet the forager does not require any direct contact with pollen to make her assessment. My experiments reveal that a forager does not assess the colony's pollen stores herself, *directly,* but rather receives information *indirectly* through other bees in the colony. It appears that the young nurse bees, whose task it is to consume pollen and feed the proteinaceous food to the developing larvae, gather information concerning the colony's pollen stores and pollen demand and then pass this information on to the foragers. In collaboration with Dr. Karl Crailsheim at the *Institut far Zoologie der Universität Graz* (Austria), we are testing this hypothesis of information acquisition. Using radioactive labelling techniques, we have obtained evidence that pollen foragers do indeed receive information about the colony's pollen reserves through the transfer of protein from nurse bees to foragers. We plan to continue this work in the summer of 1994 after my stay at the Wissenschaftskolleg.

A project I recently completed was an examination of how the characteristic concentric pattern of brood, pollen and honey develops on the combs of the honey bee colony. This colony-level pattern somehow emerges from the activities of thousands of individual bees. One possibility for how the pattern forms is that the queen and the foragers each know where on the comb to place eggs, pollen and nectar, as if each had some genetically-encoded blueprint for the pattern. In contrast to this hypothesis, I have shown that the pattern develops spontaneously through a self-organized process based on the dynamic interactions of the colony members. Though each bee acts independently, using only a few, simple behavioral rules based upon limited knowledge, an orderly pattern emerges on the comb. To explain the process of pattern formation, I first conducted a series of observations and experiments in the field and in the laboratory to determine the behavioral rules of the bees. Then, through computer simulation, I explored the implications of these rules in a model. The predictions of the model match the comb pattern seen in nature, supporting the self-organization hypothesis.

Another project involves thermoregulation in honey bee clusters. In temperate climates, a honey bee colony must survive a long, cold winter. How the winter cluster of bees regulates its temperature is another mystery of honey bee social organization. This question has attracted the attention of several investigators, especially Bernd Heinrich, who has conducted extensive experimental work on the thermoregulation of a winter cluster of honey bees. Although several models of the thermoregulatory process have been put forward, no one has yet been able to describe in detail the mechanisms involved. In collaboration with two mathematical biologists, Leah Edelstein-Keshet and James Watmough, both at the University of British Columbia in Vancouver, Canada, we have developed a model of swarm thermoregulation based upon a self-organization mechanism that links the behavior of the individual bees to the colony-level thermoregulatory response. During my stay at the Wissenschaftskolleg, we have completed this model and have written a paper summarizing our work[2].

The different defensive responses shown by Africanized and European bees also challenges our understanding of colony-level social organization. Why are Africanized (so-called "killer") bees so much more aggressive than European bees? What are the precise physiological and behavioral differences between the two races of honey bees, and how do they explain the differences in colony-level defensive behavior? If we hope to minimize the impact of Africanized bees in the United States, it is essential to understand the factors at the level of the individual that contribute to the collective defense response. In collaboration with Jean Louis Deneubourg, I am trying to develop a model which describes the

[2] Watmough, J., Camazine, S., »Self-Organized Thermoregulation of Honeybee Clusters«. *Journal of Theoretical Biology* (submitted).

factors leading to differences between the aggression of European and Africanized honey bee colonies.

Through these and other studies, a fascinating picture of social organization and colony-level structures and patterns begins to emerge. In place of centralized systems of communication and information transmission, insect societies frequently employ mechanisms based upon self-organization. I feel strongly (and I think the other members of our *Schwerpunkt* would agree) that self-organization promises to be a mechanism that will emerge as an important unifying principle in physical, chemical and biological systems. In biological systems, self-organization reveals itself as a powerful mechanism used by natural selection for the creation of diverse regulatory and morphogenetic processes.

In sum, my fellowship at the Wissenschaftskolleg has been personally very rewarding. I have been able to continue my research on self-organization, to develop new ideas, to collaborate with my colleagues, to begin writing a book devoted to self-organization in biological systems, and to lecture on this topic both here at the Wissenschaftskolleg and elsewhere in Europe[3]. But I am sure that what I will remember most in the years to come are the many interpersonal relationships that developed: the thrills and frustrations of a collaborative venture and the joys of interacting with a unique group of fellows and staff at the Wissenschaftskolleg.

[3] »Mechanisms for building organization in insect societies.« Lecture at the *Zoologisches Institut der Universität Zürich.* Zürich, Switzerland, November 1993. »Self-organizing pattern formation in honey bee colonies.« Lecture at the *Theodor-Boveri-Institut für Biowissenschaften.* Würzburg, Germany, May 1994.