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Book Review

Self-Organization in Biological Systems. By SCOTT CAMAZINE, JEAN-LOUIS DENEUBOURG, NIGEL R. FRANKS, JAMES SNEYD, GUY THERAULAZ and ERIC BONABEAU. Princeton, New Jersey: Princeton University Press (2001). Pp. 535. Price £45.00.

This book deals with self-organization in biological systems and constitutes a much-needed supplement to the mainstream treatment of behavioural ecology by Krebs & Davies (1997). In combination with *Termites, Turtles and Traffic Jams* by Michel Resnick (1994), it is an excellent textbook for courses on self-organized biological and social systems.

In an admirable way it combines detailed experiments with mathematical models of behavioural ecology. Models based on differential equations are supplemented by individual-based models in Starlogo which can be downloaded from Camazine's web site. Examples mainly concern social insects (such as ants and bees), but there are also chapters devoted to bacterial aggregates and fish shoals.

The first seven chapters describe and analyse self-organization. Examples of self-organized behaviour are set against the usual explanations, which involve a leader, a blueprint, a recipe and a template. The authors also indicate how self-organization of behaviour may be studied experimentally, mathematically and by the combination of the two methods (Chapter 6). They introduce various types of models. As regards the evolution of behaviour, they suggest that self-organization and natural selection act together and that it is through self-organization that evolution becomes truly efficient (Chapter 7).

Chapters 8–20 illustrate the process of self-organization with examples of grouping, foraging, dominance hierarchies, behavioural synchronization, building of nests and thermoregulation of swarms. The authors emphasize the operation of positive and negative feedback in all these processes. Chapter 8 shows the importance of chemotaxis (following increased concentrations of a chemical) in the life cycle of the famous slime mould, which alternates between phases in which single amoebae are solitary and 'collective' phases in which a great number of amoebae form a single, slug-like body. They describe, for instance, how a positive feedback mechanism brings (hungry) amoebae together and how this is accompanied by waves of c-AMP which may be concentric or have a spiral form (a curious difference that unfortunately is not explained).

Three of the following chapters (9, 13 and 14) continue with the effects of chemotaxis, which may lead to the clustering of beetle larvae (Chapter 9), to the efficient way in which ants forage (Chapter 13) and to the complex patterns of swarming of the huge colonies of army ants (Chapter 14). In all this both a positive and a negative feedback are involved. The positive one implies that a larger group of organisms attracts more members, because they emit more pheromone and by emitting more pheromone, again attract more members, and so on. The negative feedback is that the preference for the larger cluster (or trail) steadily increases, thus leading to the reduction of the smaller one. In this way ants select resources collectively. In a similar way, visual communication in bees via dances leads to the collective selection of a food source (Chapter 12).

In Chapter 14, the authors show in a model that different patterns of swarming result from the same path-marking mechanism in combination with different distributions of food. These patterns resemble the species-specific swarming patterns of the enormous swarm raids of blind army ants (which consist of hundreds of thousands of workers). Thus, different distributions of food rather than different behavioural rules may be at the origin of these species-specific types of swarming. Identical behavioural rules for all individuals also suffice in modelling the beautiful coordinated movements of real swarms of, for instance, fish, in spite of the lack of a leader (Chapter 11).

In Chapter 10 synchronous flashing at night of male fireflies is attributed to an optical 'coupling' mechanism, whereby each fly has its own rhythm of flashing but the sight of a neighbour's flash shifts its rhythm. In contrast to this, the remarkable capacity of honeybees to regulate the temperature of their swarms may result from the way in which individuals regulate their own body temperature, without adapting their behaviour to that of others (Chapter 15).

Chapters 16–18 treat the wonderful structures built by social insects. For instance, brood, pollen and honey are organized on the comb in concentric layers (Chapter 16). Elegant studies by Camazine and coworkers explain this pattern by self-organization. Chapter 17 describes the building of walls by ants (*Leptothorax*) that live in small crevices in rocks (the size of a wristwatch). Building mechanisms are a combination of the effects of a physical template that is due to the colony's size and of a chemical template that is due to the presence of adults and brood and they are a consequence of a positive feedback (deposited debris attracts more building material) and simultaneously of a negative feedback (clusters inhibit the building of other clusters). Apart from these mechanisms, termites also use a special 'cement' pheromone and a path-marking pheromone to adjust architecture and traffic to each other while constructing huge mounds rather like air-conditioned skyscrapers (Chapter 18).

Obviously, building is influenced by the changing environment (so-called stigmergy, Chapter 19). In a model with a rule that a cell is more likely to be built if it is in contact with three neighbouring cells than with two, artificial comb structures result that closely resemble those of real wasps.

Dominance hierarchies may influence numerous aspects of the behaviour of group-living animals, such as the reproductive physiology of female wasps (Chapter

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20). Such hierarchies may arise from a positive feedback in the so-called winner–loser effect.

Although some additions to the book would have been welcome (e.g. about dominance interactions, task division and evolution) and more mathematical details would have been helpful, the authors are remarkably successful in explaining the importance of this modern approach to science.

We must be grateful that Professor Rüdiger Wehner (University of Zurich) was aware that a book like this was thoroughly needed. As he understood the difficulty of explaining this new approach for the first time, he invited some of the authors to a sabbatical year in Berlin in order to write it.

This book is to be recommended to educated laymen, University teachers and researchers of several study areas, such as anthropology, biology, sociology and Artificial Life/Intelligence. It ought to be present on the bookshelves of every self-respecting biologist.

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