Chapter 2
A Biologically Inspired Approach to Collective Behaviors

Animal groups provide paradigmatic examples of collective phenomena in which repeated interactions among individuals produce dynamic patterns and responses on a scale larger than individuals themselves. Some of the examples around us include the coordinated movements of fish and birds in a school or a flock, respectively, the chemotactic aggregation of amoebae, the formation of lanes in densely packed human crowds, the generation of vortices in bacterial colonies, the synchronized march of wingless locusts, and the synchronized flashing of fireflies. Many more examples can also be found inside all of us: the firing of neurons in our brains, the clustering of differentiated cells to construct our organs both during embryonic development and wound healing, and the targeted response of neutrophils as part of the initial immune response to a bacterial infection. This nonexhaustive list of collective behaviors of unicellular and multicellular organisms is revealing of the pervasiveness of swarming in the natural world. Thus, there is no better place to start a book dealing with swarms (or flocks, schools, colonies, etc. [1]; the generic term "swarm" will be used interchangeably and loosely throughout this book, although in principle some differences in meanings exist) than by turning to this vast range of awe-inspiring solutions offered by mother nature.

2.1 Collective Animal Behaviors

Like the animals taking part in them, biological collective behaviors come in many different sizes and shapes (see Fig. 2.1). Some like baitballs—comprised small fish swarming in a tightly packed spherical formation about a common center—are simply mesmerizing. A very high level of spatial and social structure is not uncommon in raiding columns of army ants or termites digging tunnels in mounds. Yet other groups, like fireflies synchronously flashing, exhibit a very high degree of temporal coherence. It is crucial stressing the fact that all these self-organizing behaviors do not require any external directing influence, but instead solely emerge from repeated local interactions between swarming agents. Understanding these phenomena is a

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central endeavor at the interface of many scientific disciplines: biology, medicine, social sciences, neuroscience, to name just a few. However, throughout this book, the mechanistic aspects of collective behavior—how they are achieved—by which dynamic patterns and responses are developed and maintained are of special interest to us. More emphasis will therefore be put on these behavioral mechanisms over functional considerations—what the benefits of such group behaviors are, while always keeping in mind that mechanisms and functions are in general intertwined. This simplifying assumption is made so as to be able to establish design principles and guidelines being as general and universal as possible. Let us recall that the central focus of this book is the design and control of artificial swarming behaviors. With this goal in mind, collective animal behaviors provide a wealth of interesting case studies amenable to theoretical and numerical modeling, in other words, an inspirational gold mine.

2.2 Ethology

Ethology is commonly defined as the scientific and objective study of animal behavior, usually with a focus on behavior under natural conditions. In general, ethologists tend to favor the study of the behavioral process over an in-depth analysis of precise behavioral traits of a given species, which falls primarily into organismal biology. Given the significance of social animal behavior in nature, a large body of work in the field of ethology is dedicated to the study of collective animal behavior. These collective behaviors typically are the outcome of a suite of interactions that occur between two or more individual animals, usually conspecifics. However, at this point, it is worth distinguishing between two distinct kinds of collective animal behaviors of interest to the ethologist.

First, there are population-level phenomena whose emergence is controlled by changes in intrinsic and extrinsic factors related to ecological factors and/or evolutionary biology. For this first type of collective phenomena, the dynamics and structure of the associated social networks have far-reaching implications for the ecology and biological evolution of individuals, populations, and species [2]. For instance, the study of those phenomena allows us to understand the ability (or therefore lack of it) to adapt to environmental changes of some thriving species while others go extinct. Typically, such phenomena occur over fairly long dynamics—ranging from months to decades, or even longer periods of time for evolutionary processes—compared to the dynamics of typical behaviors occurring on a typical day.

The second class of collective phenomena, which is at the core of this book, concerns group-living behaviors such as those described at the beginning of this chapter and corresponding to short dynamics (up to a couple of days for termites digging ventilation tunnels for the mound) to extremely short dynamics (subsecond to seconds) such as in the case of a school of fish performing evasive maneuvers to escape from a predator's attack. Specifically, our primary interest lies with the dynamical aspects related to: (i) reconfiguration and response, (ii) collective information transfer, (iii) individual control laws governing the dynamics of the collective, and (iv) fast-distributed decision-making processes. There is no doubt that both classes of phenomena are intertwined: effective short-time group dynamics do provide long-term evolutionary advantages. However, in this book, we will focus our discussion on the short time, and more specifically the extremely short-time dynamic response of animal and artificial collectives, without investigating their implications at the ecological or evolutionary levels.

2.3 Why Biological Inspiration?

In this golden era of engineering design and design science, nobody would dare questioning the importance of biological inspiration. That process consists in using principles from biology to generate novel designs through integration with the most innovative human engineering. These design principles have inspired countless new designs, from new manufacturing processes, to control circuits, flying objects, self-cleaning dry adhesives, and autonomous swarm of robotic platforms. Having said that, it appears clearly that biological inspiration carries a particular significance when it comes to designing swarming systems. It is actually only fair to say that the whole notion of swarm originated from the observation of some biological systems from the animal kingdom that exhibit patterns of collective action. It is only very recently, with the realization of the importance of complex systems, that researchers considered developing artificial designs of swarms, whether in the form of algorithms or with actual agents interacting and evolving in the physical world.

Biology, and its sub-discipline ethology, are not just important because they have contributed to raising our awareness of the pervasiveness of swarms and of the considerable prospects they offer. The accumulation of empirical knowledge of animal group behavior across species is monumental owing to the dedicated efforts of scores of ethologists. This wealth of information on collective animal behavior contributes to improving our understanding of the fundamental elements underpinning the dynamics of swarms in natural systems. Among these elements are the evolutionary optimized mechanistic components responsible for all emergent collective behaviors. A detailed account of such mechanisms clearly offers an invaluable source of inspiration. Comparatively, all the scholarly research carried out to gain insight into the functional considerations of swarming, and the associated suspected benefits for the animal group, are probably of less interest to the swarm designer—unless the final objective is to devise an artificial swam that is solely limited to copying its natural counterpart. That would amount to pure biomimicry.

However, the serious difficulties faced by ethologists when trying to relate collective behavioral function and the underlying mechanisms at the individual level is revealing of one of the key challenges in swarming design: namely, to find the appropriate set of local rules, which through repeated applications, in specific environmental conditions and with appropriate agent characteristics, will lead to a desired collective behavior of interest. In itself, this stiff problem can be considered to fall in the class of inverse problems, and there is no doubt that it is a wicked problem.

As highlighted at the beginning of this chapter, collective animal behaviors represent an inspirational gold mine for designers and developers of swarming systems. For instance, insects colonies have been an amazing source of inspiration for the development of novel optimization and distributed problem solving techniques. Ants are capable of solving stiff problems far beyond the means of each individual. However, most collective tasks for which these swarming systems are developed—e.g., search and rescue operations, distributed surveillance or detection, delivery systems, etc.—are not generally performed by natural swarms, or at least not exactly in the way that the designed artificial system is intended to operate. It is therefore instrumental not being overreliant on or fixated with swarming solutions developed through millennia of evolution. This word of caution is also meant to stimulate more nonbiologically driven experiments with natural swarms. Indeed, ethologists go at great length to develop experimental setups that reproduce environmental conditions of natural swarms as faithfully as possible. Among the many difficulties faced by ethologists, the identification and tracking of every individual swarming agents is probably the most challenging, but it is required in order to understand the cohesive and dynamic response of collectives. Only with that, an improved understanding of the functions of swarming can be achieved. However, some researchers have started to carry out experiments in which collective animal behaviors arise in conditions rarely (or even never) encountered in the natural world. A good example of such experiments, would consist in constraining the schooling behavior of a collective of fish to a two-dimensional environment, e.g., by using a very shallow tank thereby preventing the three-dimensional roaming of individual school members. Despite their lack of biological relevance, these experiments could help gain new insights into the functioning of swarming systems. Not only these experiments could prove to be very valuable in that respect, but they are also probably less demanding in terms of experimental resources and could therefore more easily be carried out.

All the arguments listed above provide an overall positive answer to the question formulated in this section's title: "Why biological inspiration?" Nonetheless, one should keep in mind an important point emphasized throughout this book: the design of swarming systems is a multidisciplinary endeavor, and consequently, sources of inspiration should be sought in all fields that could potentially contribute to the successful development of a swarm. The following chapters are intended to contribute to that goal.

2.4 What Nature Teaches Us About Swarming

In this section, we will briefly review some of the central tenets of swarming that have been established through decades of rigorous and painstaking observation, experimentation, analysis, and modeling of collective animal behaviors. Of course, this review is incomplete and readers seeking an exhaustive account should consult monographs by experts specialized on this topic, e.g., Refs. [3–5]

2.4.1 Self-Organization and the Importance of Order in Life

Quite interestingly, one can say that without self-organization and swarming there would be no Life as we know it. Indeed, Life's order is characterized by a cascade of emergent phenomena; emergence being defined as the spontaneous self-organization of a system made of interacting internal agents, without intervention by external directing influences [5]. This fact was acknowledged long ago by the physicist and Nobel laureate, Erwin Schrödinger, in his distinguished monograph "What is Life" [6]. Therein, Schrödinger stressed the challenges faced by the physicist and the chemist in apprehending some of the complexities encountered in life sciences. Some of these challenges will be reviewed in Chap. 3, where the emphasis is put on collective behaviors of inanimate agents. As already mentioned and also shown in Fig. 2.1, self-organization in biological systems pervades nature and takes a central part into the morphogenesis of the vast majority of multicellular living organisms. This was recognized by Macklem [7] as one of the two secrets in Life based on Schrödinger's treatise.

To identify the central tenets of swarming, one needs to consider each and every ingredient required to produce order on a large scale, i.e., a pattern. To make matters worse and as we will see below, this order may not always be apparent. For static or dynamic patterns of self-organization to emerge, the system's components—e.g., cells, amoebae, fish, birds, or swarming agents—must intercommunicate, interact, and cooperate; these communications and interactions being typically local in the natural world. Hence deciphering emergence in a complex biological system requires a clear understanding of the following elements:

- *Interactions among agents*. They can be divided into two categories: physical and trophic. Purely physical interactions—i.e., involving any of the fundamental laws of physics, e.g., mechanical or thermal—are responsible for collective phenomena involving inanimate agents. Trophic interactions involve material flows that have specific effects on the metabolism of the recipient—typically energy, nutrients, repellents or toxins.
- *Informational exchanges*. These could be considered as a third category of interaction. In this book, we would like to draw a clear line between actual interactions and informational exchanges as the latter largely prevails in artificially swarming systems. These informational exchanges are either unidirectional or bidirectional and involve one or more sensory modalities.
- *Information processing*. The information externally acquired through the sensing of the environment and the detection of other conspecifics is internally processed through a complex and still-largely-unknown cascade of cognitive processes varying largely from taxon to taxon. Oversimplifying grossly, this process can be

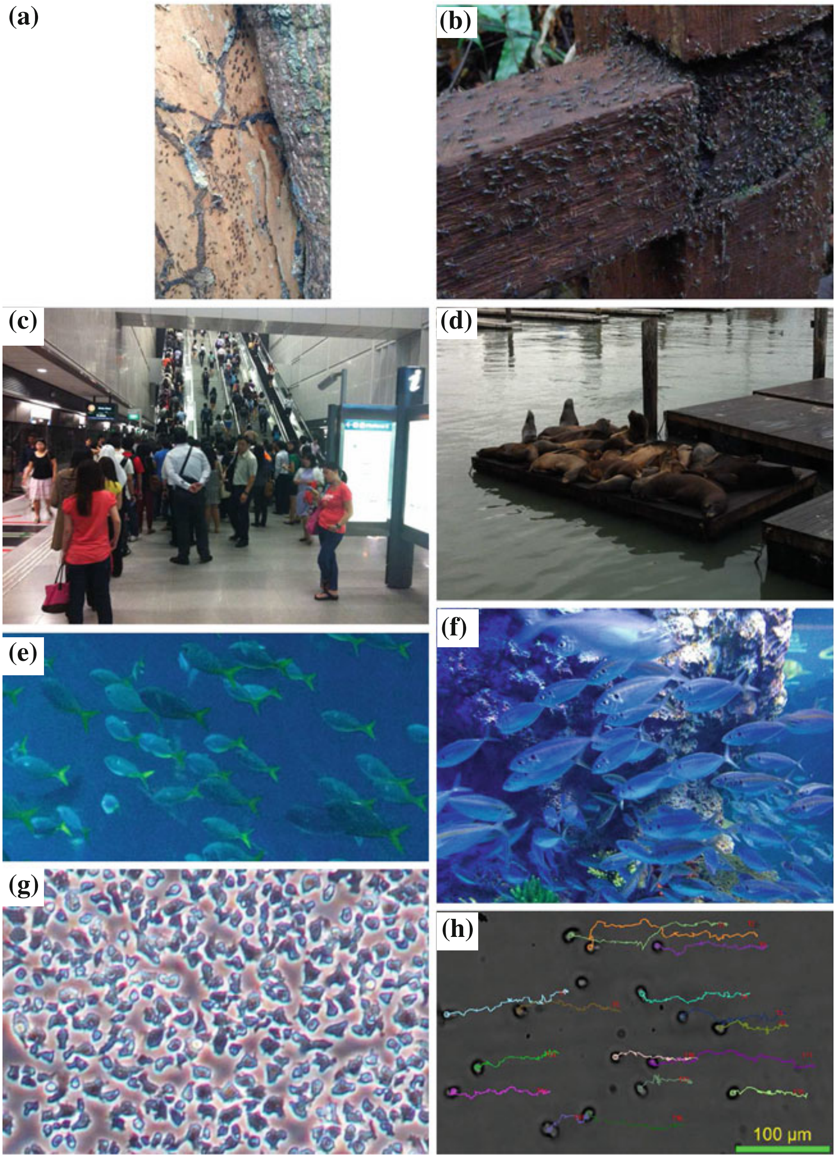

Fig. 2.1 **a** Lane of aphids collectively moving along a tree trunk (Upper Seletar Reservoir, Singapore); **b** Swarm of unidentified insects (Lower Peirce Reservoir, Singapore); **c** Lane formation in human crowds (Mass Rapid Transit station, Singapore); **d** Collective napping of sea lions (San Francisco, CA); **e** School of yellowtail fish (Pulau Besar, Malaysia); **f** School of unidentified fish (S.E.A. Aquarium, Singapore); **g** Clustered starved *Dictyostelium discoideum* amoebae (Bouffanais' lab, SUTD); **h** Mechanotactically induced collective migration of *Dictyostelium discoideum* amoebae (Bouffanais' lab, SUTD)

reduced to a filtering and integration signal processing during which salient features of the externally acquired information are extracted—e.g., sudden changes in the direction of travel are swiftly and accurately picked up by birds in a flock or fish in a school.
- *Behavioral algorithm and response*. The externally acquired and subsequently processed information is used by the animal to shape a behavioral response according to the specifics of the internally stored genetic information.

All of the above is very well summarized by Sumpter [8], who argues that the key to understanding collective animal behaviors—and more broadly the concept of self-organization and the spontaneous emergence of order—lies in identifying the principles of the behavioral algorithms followed by individual animals and how information flows between the animals.

As a matter of fact, the next chapters deal specifically with individual elements listed above. However, as is common with complex biological systems, a clear distinction between each of these elements is not always possible as they can be simultaneous and/or interwoven.

2.4.2 Positive Feedback and the Emergence of Order

Regardless of the particular level of development, the animal kingdom is filled with swarming behaviors. Among these swarming behaviors, aggregation patterns are almost universal across living organisms, from bacteria to higher vertebrates. It is now well known that these aggregation patterns as well as other forms of collective behaviors use various forms of positive feedback mechanisms [5].

A celebrated example of the importance of such positive feedback mechanism is the chemotactic aggregation of the social amoebae *Dictyostelium discoideum* (Dd). This simple eukaryote is a genetically, biochemically, and cell-biologically tractable model organism [9], which has been a microorganism of choice for studying a variety of basic processes in morphogenesis, including cell–cell chemical signaling, signal transduction, and cell motility. Of particular interest to us is the extensively studied social life [10, 11] of this prototypical motile cell. Dd exhibits a remarkable interplay between single-cellular and multicellular behaviors. Specifically, in the presence of nutrients, individual Dd cells move, feed, and divide every few hours. Food scarcity leads to a behavioral change in Dd toward a collective aggregation, which leads to a variety of wonderful complex spatial patterns. Although a complete understanding of the exact mechanisms at play during such collective aggregation remains elusive, it is generally agreed that a specific chemical, namely cyclic adenosine 3', 5'-monophosphate (cAMP) plays a central role in the orchestration of the aggregation process. This cAMP is secreted by the cells and used for intercellular communication. Without delving into the details, it has been revealed experimentally that when Dd cell sense and detect cAMP released by neighboring cells, it triggers the secretion of cAMP by the cell. In turn, this reinforces the chemical signal in the extracellular environment thereby increasing the overall signaling range necessary for the collective aggregation to perdure and for order to emerge on very large scales as observed in aggregation patterns.

In the engineering world, positive feedback loops induce amplification typically leading to a destabilization of the system. The triggering of stabilizing negative feedback mechanisms may at some point counterbalance these destabilizing effects thereby leading to a new dynamics of the system. In the example of the aggregating amoebae, some form of "recycling" of cAMP occurs to avoid a saturation in this chemical within the environment. Without cAMP recycling, cells would lose their ability to sense the chemical and detect gradients of cAMP, which would totally inhibit the aggregation process. For other collective behaviors built upon other forms of positive feedback, the counterbalancing effects of negative feedback may come from the induced depletion in resources required by the exponential growth of the system. Finally, for collective behaviors of the consensus type—a.k.a. imitative behavior such has herding, flocking schooling, synchronous flashing or rhythmic applause, etc.—negative feedback mechanisms may not be as clearly and easily identifiable.

In summary, positive feedback is a powerful mechanism to create structure and induce coherence (in time and/or space) in collective phenomena in general, and in self-organizing biological systems in particular.

2.4.3 Collective Behavior Without Large-Scale Order

All too often, collective behaviors are mistakenly associated with apparent collective order in space or collective synchronization in time. Indeed, biologists and nonexperts alike can readily detect large-scale organizations in schools of fish and flocks of birds, and also the high level of temporal coherence in the synchronous flashing of fireflies or even the rhythmic applause of audiences at the end of concerts. These patterns can be caught by the naked eye or the naked ear. However, statistical physics and the theory of dynamical systems inform us that nonapparent order may develop in interacting many-body systems. This nonapparent order is typically characterized by long-range correlations in fluctuations of the state variables. An interesting case in that respect is that of turbulent flows, which to the untrained eye appear as chaotic and lacking order. But, a fine analysis of such flows reveals the emergence of large-scale Lagrangian coherent structures associated with fluctuations of the velocity field [12]. Note that these vortical coherent structures have spectra governed by specific power laws which are the signature of a certain organization and dynamics in complex systems.

Interestingly, Cavagna and co-authors [13] have observed the occurrence of collective behaviors in swarm of insects—midges—in the absence of large-scale collective ordering. As stressed by Cavagna and his team, it is critical not to identify collective behavior with collective order. Beyond our search for universal principles in swarming, these important observations reported in Ref. [13] remind us about the vast diversity in possible swarming behaviors. The comparison between birds and flying insects thereby provides an interesting perspective. It is clear that differences in: (i) sensory modalities—amounting to differences in how information is received by each individual agent, (ii) cognitive abilities—how information is internally processed by the neural system, and (iii) behavioral response—how the agent responds to the information acquired and processed, are responsible for the emergence, or not, of large-scale order. Specifically, birds in a flock interact topologically while midges interact according to a metric distance. Moreover, the mobility of midges is far more “erratic” as compared to starlings for instance. Another interesting example with microorganisms is the chemotactic aggregation of bacteria as compared to the one of amoebae. Bacteria such as *E. coli* for instance are indirectly guided organisms [14], performing a biased random walk—through the now famous run-and-tumble kind of motility [15]—in the direction of the gradient of the chemotactic signal. Amoebae such as *Dictyostelium discoideum* are directly guided eukaryotes [16] that are able to climb fairly shallow chemical gradients with a remarkable accuracy [11]. Given such differences in sensing, processing and responses exhibited by *E. coli* and *D. discoideum*, it is therefore not surprising that their respective chemotactic aggregations are noticeably different.

We would like to return to the study of Midges in the field carried out by Cavagna and his team [13] as it calls for a new appreciation of what a swarm really is. According to Cavagna et al., the true hallmark of collective behavior in animal systems is correlation rather than order. We strongly back this view as it is becoming apparent that a too intense ordering of a swarm seems to hinder its ability to swiftly respond to fast condition changes in its surroundings. Interestingly, the new light shed on the pivotal role of high correlations in collective behaviors recalls a hallmark of complex systems, which are known to have a dynamics at the edge of chaos [17]. By that it is meant that its degree of organization lies somewhere between complete order and utter chaos. This last point will be revisited in Chap. 3.

Finally, it is worth adding that until now, this important realization about the importance of high correlations over high ordering has not been considered as a key guiding principle for the design of swarms.

2.4.4 Information Processing and Swarm Intelligence

The vital role played by information processing in the dynamics of living systems has been long acknowledged. Four decades ago, Gatlin already wrote that “Life may be defined operationally as an information processing system—a structural hierarchy of functioning units—that has acquired through evolution the ability to store and process the information necessary for its own accurate reproduction” [18]. Furthermore, information processing or equivalently computation is now known to be at the core of the dynamics of complex adaptive systems. It is therefore not surprising to find information processing as one of the central tenet of the dynamics of swarms, which are complex systems made of living units.

As was seen in the previous section, large-scale ordering may not be a true hallmark of collective behavior but it is becoming clear that large-scale information processing is one. This is readily observed in the optimal and adaptive foraging behavior of ant colonies as well as their ability to dynamically adapt to changing environmental circumstances through a fully decentralized task allocation process. Another very interesting and important example is the collective response of swarms of mobile agents exhibiting surprisingly fast responses such as dramatic stampedes in high-density human crowds, flash expansion by school of fish and collective turn by flock of birds when confronted by predators attacking. All these examples confirm the fact that information exchanges between individuals go hand in hand with some form of positive feedback: one agent imitates a neighbor's behavior, which in turn induces an imitation of other agents in its neighborhood, and thus a cascading effect typical of positive feedback ensues.

Probably, the most important difference between collective behaviors of inanimate agents (see Chap. 3) and swarms of living units resides in the ability of the latter to collectively process and respond to information in the form of signals and stimuli. There is no doubt that it contributes to the greater complexity and variety of collective behaviors observed in the natural world as compared to those encountered in the physical world. The term "swarm intelligence" is colloquially used to refer to such emergent and adaptive collective responses of groups of simple agents [19]. The past two decades have experienced substantial work aimed at mimicking specific collective behaviors of social insects. The reason for this unabated interest comes from the fact that some insects can solve stiff problems in a very flexible and robust way. Termites showcase flexibility as they are able to mend any damaged part of their mound with the same remarkable effectiveness. When ants, bees, and termites perform their unique distributed problem solving skills, they display high levels of robustness as they continue to function despite the possible loss of a large fraction of individual members. All of this with each individual insect following a very simple set of local rules and without any knowledge about the overall swarm and pattern in motion.

Robustness and flexibility are very appealing features for an engineering system. From the design standpoint, the above important facts suggest that information processing and control (i.e., the behavioral response) will be central elements to be considered and integrated into any innovative design of a swarming system.

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