CONTENTS

1

Introduction

Collective behavior is familiar, but difficult to explain. We see it everywhere in nature, and we engage in it ourselves. That you are reading this book depends on many forms of collective behavior, from the language it is in, which we acquire and maintain by using it with each other, to the paper it is on, made out of trees whose growth depends on the intricate relations of their cells. Though it is clear that collective behavior arises from interactions among the participants, it is hard to say exactly how. For example, brains work through the collective behavior of neurons. We know that neurons interact by turning each other on, but how does this produce perception, memory, and even books about collective behavior? The answer is not in the properties of individual neurons. Neurons function in brains in bodies responding to a world teeming with pattern, change, and other beings. It is these relations that generate the connections among neurons that elicit the action of each one.

Whether the whole is more than the sum of the parts is an artificial problem, created by taking the whole apart. All the king's horses and all the king's men could not put Humpty Dumpty together again, but only after he toppled off the wall; while he was alive, the cells in his shell interacted to hold him together.

The key to understanding how collective behavior works is in the dynamic relation of inside and outside rather than the assembly of parts into wholes. We are impeded by the long history that we have inherited of considering a natural system as a bounded package that

sits in a separate outside. This view leads us to account for human behavior as the actions of independent beings, propelled by internal decisions and motivations, or to partition the causes of behavior between innate or environmental. But it is not possible to learn how natural systems function collectively by considering the components separately and independently of the world they inhabit. The attempt to parse the internal and external into distinct and additive forces severs the relations that matter.

The approach I describe here has a different starting point: to explain collective behavior, it is necessary to think about how it changes in relation with the changing world it is in. I call this approach "ecological" because ecology (derived from *oikos*, the Greek word for "village") is the study of the interactions that regulate systems. It investigates dynamic systems of relations rather than sets of individuals with independent, internal properties. Versions of this, now sometimes called a "systems approach," flow through the history of the social and natural sciences.

My path to this perspective began in my second year of graduate school, when I was thinking of quitting. I had chosen to go to graduate school to learn how to do research in animal behavior and ecology because that seemed more attractive than the three alternatives I could think of: it entailed less blood than medical school, much more comfortable shoes than law or business school, and more time outside than any of the others. I had only a vague idea of what it would be like to do research. My experience of biology in undergraduate classes was mostly an effort to memorize for exams the names of parts and the little arrows connecting them—gene transcription, the Krebs cycle, photosynthesis—but these diagrams floated disconnected in a blank void in my mind, much like the white background in the textbook illustrations. Then, in my senior year, I took a course in comparative anatomy. It was a revelation to learn that the diversity of body forms in animals reflects their evolutionary history. I had been thrilled to discover, in other classes, the order in human creations, such as the counterpoint of a Bach fugue or a logical proof, but this was even more amazing: evolution generates order in a process that makes itself.

I had imagined that in grad school I would be given a lens through which I could see the processes that regulate nature, so it was baffling at first to experience the opposite. As I learned more about scientific accounts of animal behavior, it seemed that research questions were framed in a way that cut up the world into unrecognizable pieces. Behavior was portrayed as a string of prefabricated and independent snippets, and the task of researchers was to find the external switch that set off the distinct internal mechanism that initiated each snippet, or to explain why it was all for the best that the animal responded that way. An animal was a kind of windup toy, and we were looking for the key that would get it moving. But watching birds, as I did at first, or any other animals, I didn't see windup toys buzzing around. I saw rhythm, pattern, and flexibility—changing behavior linked to the behavior of others and the changing surroundings.

Each week I met with my adviser, John Gregg, and tried to talk about my sense of unease. He just smiled tolerantly and handed me books to read. One of them was Donna Haraway's *Crystal, Fabrics, and Fields*, in which I first encountered a framework and a vocabulary that made it possible to talk about my discomfort.[1] It was a great relief to discover that there was a history of thinking about biology as systems of relations. Haraway's book traces the history of the debates in developmental biology in the late nineteenth and early twentieth centuries, centered on the question of whether each cell in a developing embryo arrives at a function by following inner instructions, independently of the other cells, or instead as a result of its encounters with other cells. The debate was fueled by the opposing camps' choices of study organisms. On one side, Hans Driesch studied sea urchins, whose embryo's cells, if separated, can take on different functions, suggesting that conditions and encounters outside a cell determine its fate. On the other side, Wilhelm Roux studied frogs, in which cell function seemed to be predetermined, presumably by something inside each cell.

It was encouraging to me to learn of Driesch's perspective and the discussions it stimulated among biologists, because this suggested to me a way forward. If we could locate the cause of a cell's behavior in

its relations with other cells and the surroundings, we could think of the causes of an animal's behavior in the same way.

I didn't leave grad school. Instead, I began to study ants as a way of investigating these questions in a system where I could see what was happening as it happened. This is difficult to do in a living embryo (though the advent of the confocal microscope has now opened the way[2]). Ants are easy to watch, and even then, I knew that I learn best by seeing. Ant colonies, like embryos, operate without central control; the queen merely lays the eggs. But each one functions only in relation with the others, as Driesch saw with the cells of a sea urchin embryo.

When I began research on ants, they were viewed in scientific work as little automata, each genetically programmed to do its task, triggered by chemical cues. My first research project on ants showed that the response of an ant to a particular chemical depends on the group of ants that it is working with—either the ants collecting food or those bringing out the garbage. Thus, an ant's response depended on its relation with other ants, just as a cell's function depends on its relation with other cells. This observation meant that there was more to understanding ant behavior than identifying a chemical that acted as a switch. I was looking for a different approach.

I found ways to ask research questions that link behavior with what is around it, beginning by observing harvester ants in the desert of the US Southwest. I learned how harvester ant colonies use a network of simple olfactory interactions to regulate activity in response to changing conditions; how the ants of neighboring colonies interact to partition a foraging area; and how all of this changes over the lifetime of a colony. By following a population over generations of colonies, it has become possible to learn how natural selection from water stress is shaping each ant's response to encounters with other ants, and how this will shift as climate change exacerbates an ongoing drought. The alternative to the quest for switches that trigger isolated and fixed pieces of behavior was to follow the layers of relations and responses to changing situations.

Along the way I gave up on talking about parts and wholes, and on trying to distinguish behavior at the individual, group, or colony

level, instead asking how collective behavior at each layer is generated by interactions among participants and how this responds to changing conditions. Collaborations with mathematical biologists, computer scientists, and engineers led to quantitative descriptions of how ant colonies work. Such models, not just for ant colonies but for many other systems, show how collective behavior can be explained. We can learn enough about a system to specify how the participants interact, how these interactions are related to the current situation, and how the interactions produce the outcome.

The relation of inside and outside is always dynamic because everything changes—or, as Heraclitus put it in 500 BC (and as discussed more recently by Daniel Nicholson and John Dupre), *panta rhei* (everything flows).[3] Response to changing conditions is fundamental in living systems. Different fields of biology give this different names, such as "kinetics" in molecular and cell biology," "regulation" in physiology, or "adaptation" in neuroscience. An organism's phenotype may seem static—the flower has a certain number of petals, a person has brown or blue eyes—but even apparently static features are the outcome of some process, such as the unfolding of a flower from a bud, or the interactions among cells with melanin in the development of the layers of the iris. However any living entity may appear now, it was not always like that and will not always be the same. Change is built into life on earth, whose rotation generates the cycles of night, day, and the pull of the tides, setting up daily patterns of movement, growth, feeding, and rest. The planet's annual journey around the sun brings seasons, rain and sun, heat and cold. On a smaller scale, gut bacteria ride waves of peristalsis; blood pushes through a tangle of bifurcating tubes with each heartbeat; and molecules jiggle around causing proteins to shift their attachments.

In living systems, unlike physical ones, change goes both ways: change in any living system alters its surroundings, which in turn change the living system.[4] Newton's laws describe how an object changes position when it is subject to certain forces. These laws for inanimate objects are deterministic; the relation of mass and acceleration is

sufficient to predict how an object will move, and the surroundings are independent of the action of the objects.[5] This is never true in living systems; instead, every living entity is busy modifying its surroundings. This is easy to see in plants and animals, but equally important at every scale. For example, breast cancer cells change how neighboring cells interact with the surrounding collagen matrix and facilitate their own movement and metastasis by reorganizing the spatial pattern of cells.[6] Such mutual modification of living systems and their surroundings ripples across species. As a hummingbird flies from flower to flower and dips its beak to collect nectar, it carries microbes from the nectar of one flower to the next flower, thus changing the community of microbes living in the flowers, which in turn modify the nectar that the hummingbird eats.[7]

Here I propose that the dynamics of environments provide clues to how collective behavior operates. There are likely to be trends in how interactions generate collective outcomes, according to how the conditions in which the behavior functions are changing. The kinetics of biochemical reactions within and between cells, the regulation of physiological processes in tissues, the behavior of plants and animals in particular habitats, all reflect the way that their surroundings change. Comparative approaches in evolutionary biology show that analogous traits have evolved in relation with similar environments. Because new phenotypes tend to arise as effective responses to changing surroundings, and because adaptation leads these new phenotypes to persist over the course of evolution, similar innovations in the regulation of collective behavior should arise in conditions that change in similar ways. For example, mammals that live in cold places are likely to have thicker fur than those that live in hot places, because thick fur keeps an animal warm when it's cold. By analogy, collective behavior that responds to rapidly changing conditions is likely to use interactions that can adjust rapidly.

In *Evolution in Changing Environments*, Richard Levins outlines a general principle for explaining the evolution of phenotypic plasticity, the capacity to change in response to changing situations.[8] He argues that there is a trade-off between two costs. The first is the cost

of the work it takes to be plastic, so as to have the capacity to change when the situation changes, rather than just staying the same. The second is the cost of having a wrong or inadequate response in a particular situation. In Levins's model, the capacity to change evolves when the cost of having the wrong response in a situation is greater than the cost of the capacity to change.

This idea can be applied to the evolution of plasticity of collective behavior, the capacity to regulate or adjust collectively to the current situation. Regulation evolves when it's important to have the right response in a particular condition. Or, to turn this around, regulation that adjusts appropriately to conditions is likely to evolve. Thus, understanding the conditions to which a form of collective behavior responds suggests hypotheses about how the behavior works. For example, adrenaline influences the response to sudden change. If we knew nothing about the physiology of the adrenal system, we would guess that the processes that regulate adrenaline involve rapid chemical interactions, because the events in the surroundings that are relevant to adrenaline—such as danger—require a rapid response.

To outline correspondences between the dynamics of collective behavior and of its surroundings, I choose some features of each and suggest how they are associated. To characterize the dynamics of collective behavior—how interactions respond to changing conditions—I draw on ideas from dynamical systems and network science. I consider first, the rate at which interactions adjust to conditions, and second, the feedback regime that stimulates and inhibits a collective process. Third, I consider how participants in a collective process are linked in a network of interactions.

To characterize the dynamics of environments, I use ideas from ecology that describe three gradients in changing conditions. The first gradient is stability: how frequently and how much conditions change. This gradient includes the risk or probability of a rupture or adverse event. The second gradient is the distribution in space and time of the resources that the system uses or the needs and demands that the system must respond to. A simple version of this gradient goes from scattered or random to clustered or patchy. The third gradient

is in the energy flow that conditions allow, from a high to low ratio of energy or resources used to energy or resources taken in.

To raise new questions about collective behavior from an ecological perspective, I propose three main hypotheses, all of which suggest that, across different natural systems, similar kinds of changing conditions correspond to similar ways of using interactions to regulate collective behavior. First, the rate at which interactions adjust collective behavior is associated with the stability of the environment and the distribution of resources and demands. Second, the feedback that regulates interactions is associated both with the distribution of resources and demands and with the energy flow required to operate in that environment. Third, the modularity of interaction networks is associated with stability and the distribution of resources and demands.

To begin, the next chapter introduces these hypotheses briefly by comparing the collective behavior that regulates foraging in two ant species living in very different environments. In chapters 3 and 4, I first define collective behavior very broadly and then discuss quantitative models for how collective behavior arises from interactions among participants. In chapters 5 and 6, the ecological hypotheses are outlined in detail, with examples. Finally, chapters 7, 8, and 9 discuss the research program suggested by these hypotheses, situate this approach in current evolutionary biology, and contrast it with the prevailing one that is based on the idea that collective behavior evolves out of conflict between the interests of the individual and those of the group.

INDEX

Page numbers in *italics* indicate figures and tables.