

Measuring collective behavior: an ecological approach

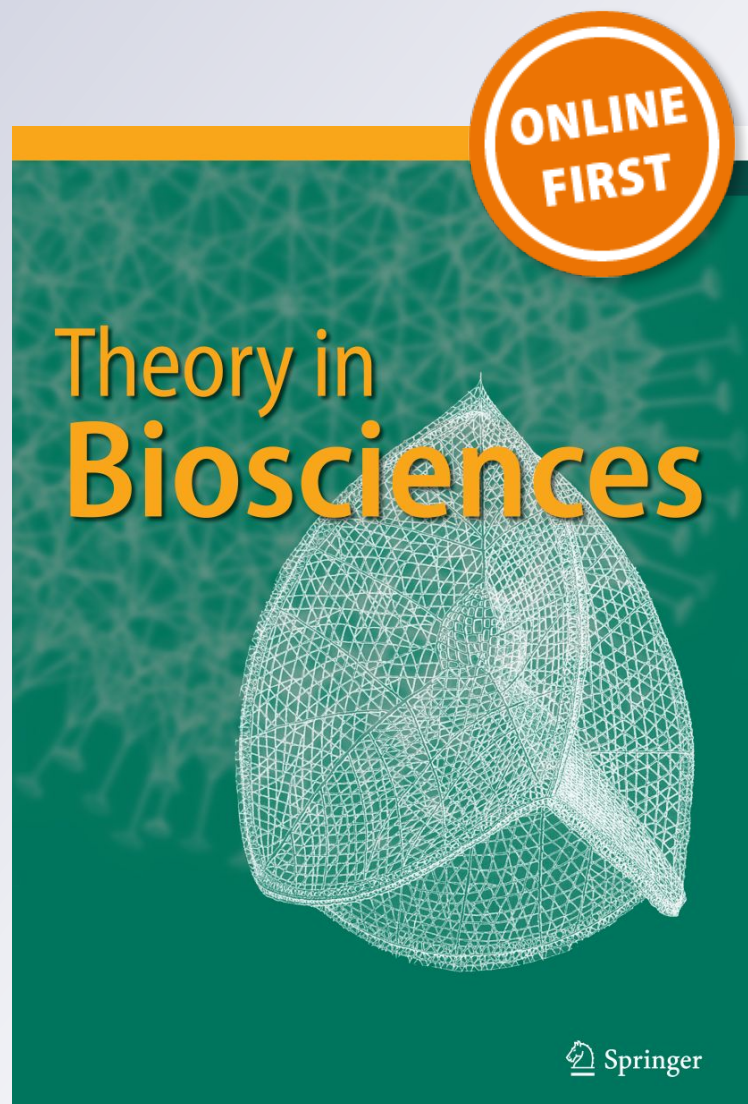
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Measuring collective behavior: an ecological approach

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Abstract

Collective behavior is ubiquitous throughout nature. Many systems, from brains to ant colonies, work without central control. Collective behavior is regulated by interactions among the individual participants such as neurons or ants. Interactions create feedback that produce the outcome, the behavior that we observe: Brains think and remember, ant colonies collect food or move nests, flocks of birds turn, human societies develop new forms of social organization. But the processes by which interactions produce outcomes are as diverse as the behavior itself. Just as convergent evolution has led to organs, such as the eye, that are similar in function but are based on different physiological processes, so it has led to forms of collective behavior that appear similar but arise from different social processes. An ecological perspective can help us to understand the dynamics of collective behavior and how it works.

Keywords Interaction network · Feedback · Social organization

Collective behavior and environment

Collective behavior occurs without central control and arises from interactions among participants. The fundamental question about collective behavior is packed into ‘arises’—how is it that the relations of participants generate the behavior of the collective? These questions arise at every scale of natural systems: How do brains remember? Why do some tumors metastasize? How does a termite colony build its mound? Early work investigating collective behavior was fueled by the hope that there would be a single general model for how interactions produce outcomes, that could be broadly applied to all collective behavior. These first models of emergence or self-organization resolved the question whether it would be possible to explain such behavior at all. By now, however, we have investigated collective behavior in many different systems, leading to many different models. It is clear that there is no single theory or model of collective behavior that applies to all the diverse forms of collective behavior that we see in nature (Gordon 2007).

I suggest that the diversity of collective behavior can provide some insight into the diversity of processes that regulate it. The many ways of producing collective behavior we see in nature, like the diversity of form and function, is the result of evolution. Collective behavior is a dynamic and functional response that evolves in relation to changing conditions. Our attempts to measure and explain collective behavior can be informed by an ecological perspective (Gordon 2014, 2016) that examines the natural history of collective behavior and its relation with its local environment. Here, I will use ‘environment’ to include everything the agents or individuals use or interact with, and everything that uses or interacts with them. The relation of behavior and environment is two-way, because behavior and environment modify each other (Lewontin 1994; Sultan 2015). How collective behavior is embedded in a system varies with physical scale. For cells, the environment is the physiological context, microenvironment, or the properties of the tissues. For ants, the environment includes the kind of habitat, the resources they use, and the place that they nest. For a school of fish, the environment can encompass an entire ocean.

I suggest that we can best understand how collective behavior works in any particular system by considering what is going on around it. That biological processes are tuned to what is outside them is a fundamental problem in explaining natural systems. In fact it is perhaps the most basic question in biology. Reductionism fails because it

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turns out that knowing all about parts does not explain what they do; the parts work together in response to each other. Thinking of the parts of a biological system as independent rarely makes sense (Barad 2007; Haraway 2016), and there are many alternatives to the idea that we can explain parts of biological systems by imagining them to be separate. Two alternative perspectives, physiology at the cellular level, and ecology at the level of individuals and groups, are both based on the effort to understand how processes are regulated inside in relation to changes in the outside. For example, physiology studies how digestive processes depend on the intake of food from the outside (e.g., Cannon 1915); ecology studies how the interaction of two species depends on the arrival of another one from the outside (e.g., Cadotte et al. 2006). Both perspectives seek to explain biological processes in relation to context.

The processes that generate collective behavior create dynamics related to the dynamics of the environment in which the behavior functions. To explain collective behavior, it is important to remember, as Heraclitus and, more recently, Nicholson and Dupre (2018) put it, that in living systems, there is always change: Everything flows. To extend that idea to incorporate environment or context is to recognize that everything flows within a system that also flows. Environments change. To quantify how collective behavior operates—that is, to identify how interactions are linked to a collective response—it helps to consider the relation between the dynamics of the behavior and those of its changing environment. We expect to find thicker fur in animals that live in cold environments and mechanisms for heat exchange for those that live in deserts. In the same way, considering the changing environment in which collective behavior operates provides hypotheses about the process that produces it.

To say that collective behavior evolves in relation to the system it is in does not rest on the belief that everything is optimal, or that the fit between phenotype and environment is perfect. Instead, I suggest that as a starting point for measuring collective behavior, it is useful to begin by considering how it is regulated, and in response to what. For example, how a school of fish turns, through local interactions among fish, has evolved in relation to events that turning is a response to, such as the appearance of a predator. To learn how a school of fish turns, and how this changes over time and differs among species, we could ask how frequent and how rapid are the events that stimulate the school of fish to turn, because these events are the context for how frequently and rapidly the school of fish responds. Collective group movement is related to ecological conditions (Farine et al. 2012).

I do not have much hope that we will ever have a general theory of how collective behavior works. But I do hope that we can discover patterns that link the process that generates

a particular kind of collective behavior, using feedback from interactions, with the dynamics of the broader system. For example, a simple version of this idea is that rapidly changing conditions will be associated with processes that create rapid adjustment, while very stable conditions will be associated with processes that allow for slow change.

The question, then, is whether there are general correspondences in the diversity of collective behavior and the diverse dynamics of the environments in which it occurs. One way to proceed is to begin with a taxonomy that matches up the relevant properties of changing environments, and those of collective behavior. There is no rigorous ecological or physiological theory that could specify which aspects of changing conditions must be relevant, but we can look for analogies between many different systems that suggest similarities in the correspondences between collective behavior and its surroundings. In previous work, I have suggested some examples from evolutionary biology (Gordon 2014), cellular systems in Gordon (2016), and the collective behavior of ants (Gordon 2018).

Some of the features of changing environments that seem to be important in shaping collective behavior are stability, constraints on energy flow, the distribution of resources, and the risk and cost of threats (Gordon 2014). Stability is how quickly the environmental conditions change, relative to the timescale at which the collective behavior responds. Constraints on energy flow correspond to how much the system has to spend in relation to what it gains. Resource distribution includes how scattered or patchy are the resources in space and time. Finally, both the risk and cost of threats can vary; how frequent are threats or interruptions to the system, and how likely they are to obstruct or destroy it.

The dynamics of the environment are reflected in the processes that regulate collective response to these changing conditions (Gordon 2016). There seem to be some general features of the dynamics of collective behavior that match the conditions in which they work. One important feature of the dynamics of collective behavior is its capacity to amplify, for example to amplify activity (Daniels et al. 2016). Another is the form of feedback or control (Leonard 2014), which determines how difficult the behavior is to initiate and how easily it can be inhibited. For example, the feedback regime determines whether the default state is to be inactive, unless stimulated to begin, or instead to be active, unless inhibited and forced to stop.

Collective behavior is always a response to changing environmental conditions. For example, the collective behavior of cells shows a range of dynamics linked to changes in the microenvironment and the behavior of other cells (Gordon 2016). The development of new hair follicles depends on slow movement, on the timescale of weeks, in response to seasonal changes in temperature that shaped the evolution of hair growth. By contrast, in response to a wound in the

skin, epithelial cells move quickly, using rapid interactions, to close the wound on the timescale of minutes and hours. In cancer biology, it is clear that outcomes depend on interactions of cancer cells and healthy ones; whether a tumor metastasizes depends not just on how many cells have certain cancer mutations but on how the cells interact with each other and healthy cells so as to regulate their movement and proliferation. A current frontier in cancer research is asking how the dynamics of tissue environments affects the rate of evolution of particular cancer genotypes, for example how the rate of chemotherapy influences the evolution of drug-resistant tumor cells (Maley et al. 2017, Chowell et al. 2017).

How interactions generate collective behavior

Measuring collective behavior—like measuring anything else—requires decisions about what to observe and how (Martin and Bateson 1993). Some of the issues that arise in measuring collective behavior are common to any study of behavior. The most fundamental problem in quantifying behavior is that behavior happens over time and so requires methods that deal with its dynamics. All measurement of behavior is a sample of an ongoing process. Altmann's seminal paper (Altmann 1974) lays out the basic issues of this sampling problem by distinguishing between 'focal' and 'snapshot' sampling. Focal sampling follows particular individuals, while snapshot sampling describes the behavior of a set of individuals at a particular time. Focal observations track what a neuron, cell, fish, bird, or ant is doing, while snapshot observations describe something about all of them, and the relation among them, at a given time. For example, to track the position of a starling in a turning flock requires focal observations of one starling at a time, while snapshot observations measure the positions of many starlings to map their configuration. In the study of collective behavior, the goal is to understand how it works. This requires measuring the behavior of the group but also the interactions that generate that behavior. Thus, to understand how interactions among the starlings allow them to turn, both focal and snapshot observations are needed—measures of the trajectories of many starlings, and the configurations of starlings at many time points, as the configurations change. These observations then make it possible to ask how the starlings interact and how this influences each starling's movement.

We can consider collective behavior at two levels. One is the collective outcome, what the group does, how it varies and how it responds to changing conditions. In the dramatic and well-known cases of collective movement, the collective outcome is obvious: The flock of birds turns in the sky; the school of fish splits and then fuses. Flocks of birds turn

in response to some events that lead some of them to shift position, leading others to respond.

But often it takes a shift in perspective to see behavior as collective. What is required is stepping back, or zooming out, to look at the behavior of different individual agents in combination and see it as a pattern generated by interactions. Once we see that a group of individuals, such as cells or ants, are acting collectively, responding together in some way to changing conditions, the next step is to ask how the individuals interact so as to produce this collective outcome. That is, what is the process that links interactions among individuals, and changes in interactions in response to conditions, to create the feedback that influences individual behavior so as to produce the collective behavior?

Once we have model or description of the process that uses interactions to generate the collective outcome, it cannot be taken for granted that this process actually does produce the observed outcome. There are in principle an infinite number of different processes that could yield a given outcome. It is rarely possible to prove rigorously that a given model corresponds to the process at work in nature. But the more ways that a model predicts changes in outcome as a response to changing conditions, the more convincing is the fit between model and observation. Often the most important contribution of a model is to show us where we are wrong and to inspire further observations to refine the model.

Collective behavior in ants

In practice, measuring collective behavior in ways that help to explain it requires iterations around a loop: identifying the pattern in behavior or collective outcome, tracking the interactions that produce it, seeing how the collective outcome changes in different conditions, testing how the interactions depend on conditions, and then considering variation in response to conditions, what in evolutionary biology is called a 'reaction norm.' Here, I describe some examples of this process from my work on ants.

Ants provide opportunities to map the fit between the dynamics of changing environments and the dynamics of collective behavior (Gordon 2019). There are more than 14K species of ants that have evolved to work collectively in every conceivable habitat on Earth. All ant species live in colonies that operate without central control. Colonies consist of one or more reproductive females who, although they are called 'queens,' merely lay the eggs and do not direct the behavior of the workers who are sterile females. The collective behavior of an ant colony is the aggregated behavior of many ants, each responding to the conditions it experiences and to the others that it encounters (Gordon 1996, 2015).

The interactions among ants that regulate collective behavior are mostly olfactory. Antennal contact is a

common form of interaction among ants. An ant's odor comes mostly from a layer of greasy lipids, cuticular hydrocarbons, smeared on its body by grooming. Ants smell with their antennae, and when one ant contacts another with its antennae, it assesses the odor of the other. We learned this from experiments in which we coated glass beads with the cuticular hydrocarbon extracts and introduced the beads to the nest. We found that ants responded to the rate at which they contacted the glass beads, smelling the hydrocarbons on the beads, in the same way that they responded to interactions with ants (Greene and Gordon 2003). This showed that the ants are using the rate at which they meet and that there is no other message besides the odor of the other ant.

Another familiar olfactory interaction uses a chemical cue left on a substrate by another ant; for example, in some ant species, one ant puts down a volatile trail pheromone as it walks, and another comes along and smells it. This is an olfactory interaction with a short time lag. That ants use trail pheromone was shown by observations of ants walking on a glass plate covered with charcoal dust, on which it was possible to see the tracks of ant abdomens as they deposited pheromones, and by extracting the contents of glands in the abdomen and observing the reaction of ants to pieces of paper soaked in the those pheromone secretions (e.g., Wilson 1962).

Measuring collective behavior in ants, as in any other system, requires both focal and snapshot observations. I began to suspect that ants use interaction rate to regulate collective behavior in my early work on harvester ants (Gordon 2010). First, I found that perturbations that change the activity of ants performing one task led to changes in the activity of others. This involved snapshot observations, in the form of a series of counts of numbers of ants performing each task throughout the morning. I made counts for many colonies on the same day since activity varies both among colonies and in response to day-to-day changes in weather (Gordon 1987). I then created perturbations that affected only the ants engaged in a single task. When I put obstacles on the foraging trail, which slowed down but did not stop foraging activity, more ants did nest maintenance work. When I put out small piles of toothpicks near the nest entrance, which stimulated more nest maintenance workers to move them out of the way, fewer ants foraged. Focal observations of foragers and nest maintenance workers, marked according to their task with paint, showed that these tasks were performed by different ants (Gordon 1989). These results, showing that events affecting one group of workers changed the activity of another group of workers, meant that the two groups of ants must interact somehow. Since the ants of different task groups were not in contact outside the nest, they must interact inside the nest. Other experiments showed that the responses to perturbation showed a nonlinear dependence on colony size, with more stable and homeostatic responses in

larger colonies. Again this suggested that the rate of interaction must be important, since colony size influences the numbers of ants available to interact.

I then began to consider what determines the rate of interaction. Since path shape determines interaction rate (Adler and Gordon 1992), and interaction rate depends on density (Davidson and Gordon 2017), ants might use interaction rate as a cue to density; that is, interaction rates can provide feedback on the numbers performing a task. Experiments with other ant species supported this (Gordon et al. 1993); for example, Argentine ants can regulate collective search according to the density of searchers (Gordon 1995). The use of interaction rate as feedback is widespread in many biological systems. Recent work shows that interaction rates are used as a cue to numbers present by acorn ants (Sasaki and Pratt 2018) or honey bees (Marshall et al. 2009) as they choose a new nest. Similarly, bacteria use the amount of chemical secreted by others as a cue to density in quorum sensing (Miller and Bassler 2001).

The collective regulation of foraging in harvester ants

Measuring the foraging activity of harvester ants led to investigating how it is regulated using interactions. The foraging activity of a harvester ant colony can be measured as the number of ants currently foraging. This species eats seeds that are widely scattered by wind and flooding, so they do not recruit each other using pheromone trails. Foragers leave the nest in streams of ants that then scatter to search individually for seeds. To learn which ants forage, and in what conditions individuals shift from one task to another (Gordon 1996, 2015), we made focal observations by marking individuals with colored paint (Gordon 1989). We measure the collective outcome, foraging activity, by measuring foraging rates. These are a series of continuous snapshot observations. We count the numbers of foragers traveling in and out of the nest per unit time, either by watching the ants go by and recording every time an ant goes by in a given direction (e.g., Gordon 1987), or by videotaping the trail and using image analysis software to do the same thing (e.g., Prabhakar et al. 2012).

Harvester ants regulate foraging activity in response to changing conditions. Over the course of a morning in the summer, foraging activity shows a temporal pattern. Activity begins after sunrise when the sun warms the nest entrance, reaches a steady peak in mid-morning, and ends at about noon when temperatures rise and humidity declines. Foraging activity changes from day to day, as weather and food availability shift.

Foraging activity is regulated by interactions inside the nest. An outgoing forager uses its rate of interaction with

returning foragers with food in its decision whether to leave the nest on its next trip to search for food. Each forager searches until it finds food, so the greater the food availability, the faster foragers find food and the faster they return to the nest, and the more foragers leave to forage. Thus, while no individual can assess food availability, interactions with returning foragers generate feedback that is linked to food availability.

Perturbation experiments were needed to learn that interactions between outgoing and returning foragers are crucial in stimulating foraging activity. When returning foragers were removed, the rate at which outgoing foragers leave the nest on their next foraging trip slowed down (Gordon et al. 2011). We then produced a model that predicted the rate at which foragers leave from the rate that they return (Prabhakar et al. 2012). We found that simulated rates of outgoing foraging, in response to observed rates of forager return, matched well with observed rates of outgoing foraging.

The next step was to examine how individuals respond to interactions. First, we tested whether outgoing foragers respond to the odor of returning foragers, the food they carry, or both, using small silica chips coated either with forager cuticular hydrocarbons, oleic acid (found in seeds), or both. We found that foraging response was stimulated only by both; outgoing foragers require both the odor of the returning forager and of the food it carries (Greene et al. 2013). We then developed a method to measure interactions in the field by uncovering the underground chamber, the 'entrance chamber,' where returning and outgoing foragers interact, and videotaping the behavior of undisturbed foragers. By tracing the trajectories of foragers and all of their interactions, we could identify the time course of interactions. We found that the higher the rate at which returning foragers enter the nest, the more interactions the outgoing foragers experienced. We performed perturbation experiments, removing the returning foragers for different intervals, and found that when no foragers return for more than about 8 min, ants in the entrance chamber return to the deeper nest where they are not available for foraging (Pinter-Wollman et al. 2013). Another study of foragers inside the entrance chamber showed that changes in the rate of forager return influence how ants come up from the deeper nest and return to it (Pless et al. 2015).

These results led to a model for how individual ants assess their rate of interaction. We modeled the response of outgoing foragers to antennal contact as a 'leaky integrator,' by analogy with a neuron (Davidson et al. 2016): Each interaction, in the form of an antennal contact with a returning forager carrying food, stimulates a neurophysiological response that decays over time. If the ant experiences enough interactions before the last ones 'leak' away, the ant is likely to leave the nest to forage. We found that a

leaky integrator model fits the data and could predict when an ant would decide to leave the nest.

Once we knew how one forager is stimulated to leave the nest through its interactions with others, we could model the entire process that regulates foraging activity (Pagliara et al. 2018). Using the tools of control theory, we describe the interactions of foragers inside the nest as closed-loop excitable dynamics: The return of foragers with food stimulates more foragers to leave the nest to search for food. This is an open loop. Then, the outgoing foragers close the loop by finding food and bringing it back to the nest, stimulating more foragers to leave.

This leads to evolutionary questions: How does the regulation of foraging respond to changing conditions, how does that vary among colonies, and how that is shaped by natural selection? During the course of the foraging period each morning, temperatures rise and humidity falls. Foraging activity decreases as humidity falls (Gordon 1986), as foragers become less likely to leave the nest (Gordon et al. 2011) until eventually foraging activity ceases during the midday heat (Pagliara et al. 2018). Foraging activity varies from day to day in response to changing weather conditions, e.g., (Gordon et al. 2008, 2011). Colonies differ in how they regulate foraging. These differences are most apparent on days when humidity is low. Some colonies were observed to reduce foraging more in dry conditions, while others continued to forage despite low humidity (Gordon et al. 2011; Gordon 2013). Colony variation in foraging activity persists from year to year, although workers live only a year (Gordon et al. 2011). This suggests that successive cohorts of workers inherit similar responsiveness to social interactions and to humidity.

Colonies that regulate foraging so as to reduce foraging and conserve water on dry days were more likely to produce offspring colonies. Thus, the more successful colonies sacrificed food intake to conserve water by restricting foraging activity that entails evaporative water loss (Gordon 2013). It seems that the variation among colonies, on which selection is acting, arises from variation in worker neurophysiology associated with biogenic amines such as dopamine, which appears to be related to forager sensitivity to humidity (Friedman et al. 2018, 2019). The study of colony reproductive success was done during a time of severe drought, and we are now hoping to learn whether, in more humid condition, selection continues to favor low foraging.

The diversity of collective behavior in ants

Comparing species shows how environments shape the processes that generate collective behavior. For example, the regulation of foraging by harvester ants differs greatly from

the regulation of foraging trail networks by turtle ants in the canopy of the tropical forest of western Mexico.

Turtle ants (*Cephalotes goniodontus*) live in the trees in tropical forests, a rapidly changing environment where it is easy to move around, since the air is humid, and there are many threats from competing species. The ants are arboreal, never coming down out of the tangle of bushes, trees, and vines of the canopy of the forest, where they nest and collect patchy resources such as nectar from clusters of flowers. They forage by forming a network of trails within the vegetation. A colony has several nests in branches of dead wood, and the colony maintains a routing backbone or circuit of trails that link all of these nests, with other temporary trails from the main circuit that extend to food sources.

A turtle ant puts down pheromone as it walks along, and at each junction in the vegetation, an ant's choice of path depends on what most of the ants did that recently passed by, because it tends to take the path that is the most reinforced by pheromone. However, occasionally some ants take another path, not the one most reinforced. Such exploration is what allows the colony to find new resources and to create new paths that repair paths ruptured by breaks in the vegetation due to wind, rotting branches, wind or animals passing through (Gordon 2017).

To measure the trail networks, I marked each junction in the vegetation network where the ants chose a new edge and monitored these day after day to see how quickly it changes (Gordon 2017). I also marked individual ants, painting their heads with colored nail polish, to see how individuals change paths (Gordon 2012). To learn how they repaired the trails, I then did perturbation experiments, cutting a stem on which the ants were passing and tracking the new trail that formed to bypass the rupture. To find out how often ants leave the trail to explore, I first put out baits to see how quickly ants found them and then observed how long it took before an ant passed by a junction a given number of junctions from the main path (Gordon 2017). It is not possible to monitor the chemical interactions between ants directly, because we cannot detect pheromone in the small quantities in which it is deposited. Instead, to learn about the rate of pheromone decay, we measured the interval elapsed between the last time an ant passed a junction and the first time another ant arrived at that junction and appeared to have no pheromone trail to guide it, hesitating and moving back and forth among the possible edges (Chandrasekhar et al. 2018).

We then created a model to identify how turtle ant foraging networks are created and maintained using interactions based on trail pheromone. Using these measurements, we were able to model a simple algorithm that reproduces much of the trail network dynamics (Chandrasekhar et al. 2018). It has only two parameters: the rate of exploration and the rate of pheromone decay. The parameter values for exploration probability and pheromone decay that were most successful

in simulation correspond to the ones we derived from the observations. We are now working to incorporate the effects of the spatial heterogeneity and the network topology of the vegetation.

The collective behavior of turtle ants and harvester ants show dynamics that fit the environments in which they evolved. Harvester ants live in a stable but harsh desert environment in which water is limited, and there are few threats from other species. An ant loses water to evaporation while out in the sun searching for seeds and colonies get water by metabolizing the fats in the seeds they eat. Thus, a colony must spend water to obtain water and food. How a colony manages this trade-off, using interactions inside the nest to adjust foraging to current food availability and conditions, is crucial for its reproductive success (Gordon 2013). The collective regulation of foraging by harvester ants in a stable environment, seeking scattered resources, with limited water and thus a high cost of foraging, is slow, not easily amplified and without recruitment. The process uses feedback that sets the default at no activity; ants do not forage unless they experience interactions associated with food availability. The information is exchanged only at the nest. Because each foraging trip takes about 20 min, this spatial centralization of information produces a slow collective response.

The collective regulation of foraging by turtle ants in an unstable environment, with a low cost of movement but high competition, is rapid, easily adjusted to recruit to patchy resources, and uses feedback that sets the default to keep going; they continue activity despite ruptures and obstacles, unless there is a disastrous encounter with a competing species. Information is regulated locally, at every junction in the vegetation, which allows for rapid adjustment of the trail network.

Ants provide many other examples of this fit between the dynamics of the environment and the process that regulates collective behavior (Gordon 2018). For example, acorn ants live in acorns or other small cavities that frequently rot or are destroyed. The process that regulates the collective choice of a new nest favors rapid emigration over optimizing nest quality. Interactions between scouts and ants back in the nest create feedback that easily provokes the decision to move, so that the default is to go rather than to wait for the best possible new nest. Another example of rapid amplification, feedback that promotes further activity, and the use of local rather than spatially centralized information comes from leaf-cutter ants. They gather leaves or grass to feed the fungus that they eat. Interactions along the foraging trails allow them to remove obstacles and to adjust very rapidly the flow of traffic and the choice of vegetation. Of the 14K species of ants, only about 50 have been studied in detail, so there are many opportunities to learn how the processes that generate collective behavior from interactions have evolved in diverse environments.

Conclusion

Situating collective behavior in a changing environment can provide a biologically realistic perspective on how it works. Specifying the processes that generate collective behavior is an iterative process that involves asking the same questions and then using the answers to reframe them and ask again: What are the individuals doing? What is the collective pattern their behavior generates? What are they responding to? How do they interact? An ecological perspective considers these questions in relation to the rest of the system, considering how the system changes and how the behavioral outcomes respond. There may be no general theory that will predict all of the processes that allow natural systems to operate without central control. But we know that collective behavior evolves in relation to an ecological context, and this can help us to discover the diverse processes that generate collective behavior from simple interactions. To understand collective behavior, we need studies that measure collective behavior in the context of changing conditions.

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