

Collective behavior in relation with changing environments: Dynamics, modularity, and agency

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Abstract

Collective behavior operates without central control, using local interactions among participants to adjust to changing conditions. Many natural systems operate collectively, and by specifying what objectives are met by the system, the idea of agency helps to describe how collective behavior is embedded in the conditions it deals with. Ant colonies function collectively, and the enormous diversity of more than 15K species of ants, in different habitats, provides opportunities to look for general ecological patterns in how collective behavior operates. The foraging behavior of harvester ants in the desert regulates activity to manage water loss, while the trail networks of turtle ants in the canopy tropical forest respond to rapidly changing resources and vegetation. These examples illustrate some broad correspondences in natural systems between the dynamics of collective behavior and the dynamics of the surroundings. To outline how interactions among participants, acting in relation with changing surroundings, achieve collective outcomes, I focus on three aspects of collective behavior: the rate at which interactions adjust to conditions, the feedback regime that stimulates and inhibits activity, and the modularity of the network of interactions. To characterize the dynamics of the surroundings, I consider gradients in stability, energy flow, and the distribution of resources and demands. I then propose some hypotheses that link how collective behavior operates with changing environments.

KEYWORDS

ants, collective behavior, harvester ants, turtle ants

The collective behavior of any natural system is the outcome of interactions among individuals and with their surroundings. An embryo grows as cells interact in relation with each other and the conditions around them; an ant colony forages as ants interact with each other and their environment. To explain how collective behavior works is to specify how the participants interact, how those interactions respond to changing conditions, and how that generates the collective outcome (Ouellette & Gordon, 2021).

While the first step in learning how a natural system works is to identify its parts and the mechanisms by which they interact, this is never sufficient to explain or predict the behavior of the system, because its behavior depends on what is happening around it. It is becoming apparent that in many fields of biology, an outstanding problem is the relation of inside and outside, that is, how the parts of the system interact so as to respond to and modify their surroundings (Laland et al., 2014). For example, the field of eco-evo-devo asks how conditions

influence development and how this relation evolves, or studies of phenotypic plasticity examine how the form, physiology, and reproductive cycles of organisms change in relation with conditions.

As biology expands its perspective, we are working to find the language with which to talk about natural systems in ways that join inside and outside, organism and environment, cells and their surroundings. To discuss collective behavior and its surroundings, I refer to the relation of behavior “with” rather than “to” its surroundings, as a way to emphasize the two-way relation itself rather than the effect of one side upon the other. This is an attempt to join them together, recognizing that it is almost impossible to find ways to talk about inside and outside, as in organism and environment, or cells and tissues, without separating them. Even the word “interaction” sets up the actors as distinct so that the action happens in the region between them, the “inter.” Latour (1993) traces this problem back to the Enlightenment and the separation of the observer of nature from nature itself. One starting point for the contemporary effort in evolutionary biology to link inside and outside was Lewontin's (1983) coupled differential equations that go from organism to environment and from environment back to organism. Formally this refers to a relation, but the two sides, organism and environment, are still each stranded on their own on either side of the equals sign. Finding ways to talk about process and surroundings together is a work in progress throughout biology.

In this essay, I will use examples from ant behavior to outline some general hypotheses about how collective behavior is likely to work in relation with a changing environment. All species of ants live in colonies consisting of one or more reproductive females and many sterile female workers. Since colonies produce other colonies, a colony is a reproductive individual. Although the reproductives are called “queens,” they merely lay the eggs; they do not have any authority and do not direct the behavior of other ants. Ants use local interactions, mostly olfactory and tactile. While ants of most species can't see, all species rely on smell, with the capacity to distinguish hundreds of odors.

Many studies show that the collective behavior of ant colonies, like that of all natural systems, is regulated in response to changing conditions (e.g., Alma et al., 2016; Bollazzi & Roces, 2007; Pereyra & Farji-Brener, 2020). The next question is whether there are trends or patterns across systems in the association of collective behavior with particular kinds of ecological situations. Here I propose several hypotheses about general ecological trends in how collective behavior is regulated in relation with changing conditions. How quickly the interactions shift as conditions change, how they stimulate or inhibit activity, and which participants tend to interact with

others, are all likely to reflect the dynamics of the environment.

To illustrate these ideas, I will compare the collective foraging behavior of two species of ants, turtle ants (*Cephalotes goniodontus*) and harvester ants (*Pogonomyrmex barbatus*), that live in very different environments. Harvester ants live in the desert, where the surroundings and the availability of resources change slowly, and they must regulate foraging so as to manage water loss. Turtle ants live in the tropical forest, in the rapidly changing tree canopy, where they forage for patchy and ephemeral resources, and where activity is easy in high humidity.

Harvester ant colonies adjust foraging activity in response to humidity and to the availability of food (Pagliara et al., 2018). Water is scarce in the desert. Because ants lose water to evaporation while out foraging, and get water from the seeds they eat, colonies face a tradeoff between spending water while searching for food and obtaining food and water.

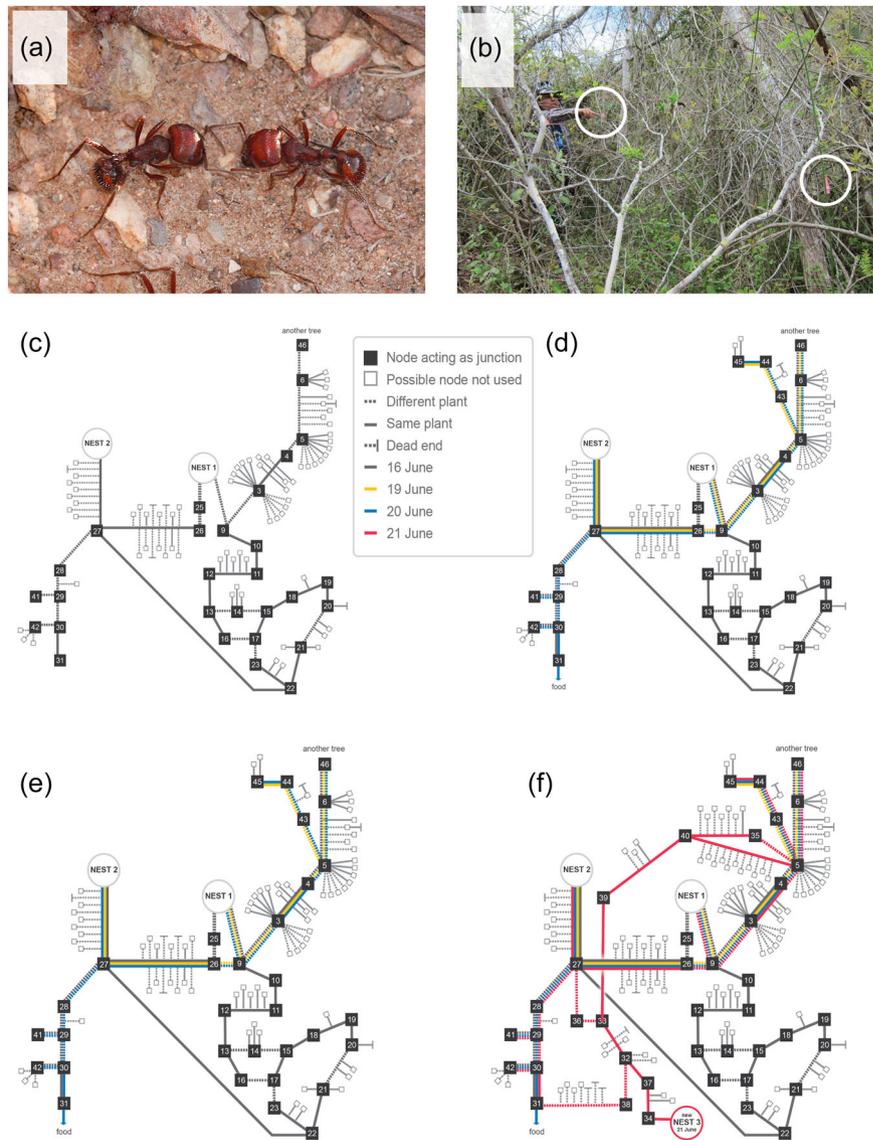
Harvester ants manage this tradeoff, regulating foraging activity from day to day and hour to hour, using feedback from brief antennal contacts. Ants smell with their antennae. Like many insects, ants' bodies are coated with waxy cuticular hydrocarbons, which they spread on themselves and others by grooming. Cuticular hydrocarbons help to prevent desiccation, and vary in odor among colonies and among task groups within colonies. When one ant touches another, it assesses the odor of the other ant's cuticular hydrocarbons (Figure 1a).

A harvester ant forager does not leave the nest until it meets enough foragers returning back to the nest with food (Davidson et al., 2016; Pinter-Wollman et al., 2013). Because each forager searches until it finds food, this positive feedback from returning foragers links foraging activity to the current availability of food: the more food is available, the shorter the search time, the more quickly foragers return, and the more foragers go out to search.

The desert environment of harvester ants is stable with respect to their resources, the seeds of annual plants, whose distribution and abundance changes on the timescale of weeks and months as seeds are scattered by wind and flooding. Within a day, the rate of antennal contact in the nest between outgoing and returning foragers adjusts to conditions slowly. Foraging activity does not change from hour to hour very rapidly, and the magnitude of change is low. Foraging activity, which spends water in evaporation from searching foragers, is suppressed unless there is enough food to make it worthwhile given day-to-day changes in humidity.

Ants must come close to each other to engage in antennal contact. The intersecting paths of ants as they meet, touch antennae, and then move on, create a network of interactions (Davidson & Gordon, 2017). The

FIGURE 1 (a) Antennal contact in the harvester ant, *Pogonomyrmex barbatus*. (b–f) Show changes in the trail network of a colony of the turtle ant, *Cephalotes goniodontus*. Each figure shows the trails on a different day over the course of 5 days. In diagrams (c–f), numbered squares represent nodes in the vegetation where ants choose from at least 2 further pathways. The photograph in (b) shows the new path represented in red in (f); node 5 is on the left and the new nest is circled on the right. [Color figure can be viewed at wileyonlinelibrary.com]



interaction network that regulates foraging in harvester ants has low modularity. The antennal contacts between returning and outgoing foragers are centralized in the single entrance chamber of their nest; each ant must complete a foraging trip before its behavior has any impact on the behavior of others. Interaction networks with low modularity spread information slowly across the network (Meyers et al., 2006), because the lower the modularity of a network, the more links it has, and it takes time to travel along the links (Clune et al., 2013). For harvester ants, a system with low modularity, in which information about food availability spreads slowly, fits a food supply that does not change rapidly. Low modularity in an interaction network, when each participant is equally connected to others, also spreads information broadly (Newman, 2018). Regulation from the central nest means the colony searches for scattered seeds without any explicit spatial information about the

location of seeds (Prabhakar et al., 2012). An ant returning with a seed from one direction can stimulate a forager to go out to search in another, so interactions inside the nest spread information throughout the foraging area. This fits a food supply in which resources are scattered, not clustered, so that it is equally useful for the ants to search anywhere so as to cover the entire foraging area.

In contrast, turtle ants regulate foraging in the frequently changing vegetation of the tropical forest. A colony maintains a set of trails through the tangled vines and trees of the canopy. In this species, unlike harvester ants, a colony has many nests, each with brood (Powell et al., 2011). Trails link all of the colony's current nests together and also have temporary trails to transient food sources, such as nectar in flowers (Gordon, 2012, 2017). The crucial olfactory interactions involve a volatile trail pheromone. Turtle ants deposit pheromone as they walk,

not just after they have found a food source. At a junction, where an ant has a choice of paths out of the junction, such as a node at a stem with other small branches coming from the node, the ant is likely to choose the path where most ants have recently passed by and deposited pheromone. The vegetation that forms the nodes in the ants' trails, such as vines and their tendrils, and the stems and leaves of annual plants, trees and bushes, changes frequently on the spatial scale at which they present options to the ants traverse them. Which stems and branches form junctions can change from hour to hour and day to day, as plants grow, the wind moves leaves and branches around, and passing lizards and birds shift the tangles of vines.

In this unstable and patchy environment, a colony's trail network changes from day to day (Figure 1b–f; Gordon, 2017). The turtle ants adjust the trail using local interactions based on the pheromone level on each available path out of a junction in the vegetation. This allows for rapid adjustment to ruptures such as broken branches, and for collective search for new food sources and nest sites. With some small probability, an ant is likely to take a path that is not the most strongly reinforced. Usually, an ant turns back when it reaches a junction where other ants have not traveled recently, but sometimes it does not. It may continue to a new food source, and when it returns, others may follow, eventually creating a path to the food. That ants sometimes choose the trail not reinforced, behavior that could be considered exploration or a mistake, allows the ants to repair ruptures in the trail. Ants respond to a rupture by searching at the node nearest the break (Gordon, 2017). Once ants from both directions find a segment that connects, they reinforce it with pheromone and thus link the two broken ends of the circuit. This local regulation allows the ants to maintain and repair the trail quickly and locally, without any need to travel back and forth from a central nest for information exchange.

In contrast with harvester ant foragers, who remain inactive unless something triggers foraging, the default for turtle ants is to continue activity on the trails unless something stops it. Ants keep moving along, reinforcing the trail unless activity is inhibited, either by a hostile presence such as a predator or by congestion at the nest.

Also unlike harvester ants, interactions among turtle ant foragers are highly modular; the ants near each other at a junction are more likely to interact with each other than with the foragers elsewhere on the trail. Modular systems allow for local innovation, in this case, the formation of new trails, because ants nearby reinforce the trails with pheromone. In addition, turtle ants use a modular form of search. When an ant at a junction

chooses a path that is not reinforced by pheromone, it usually goes back and forth on that branch and on the other branches or stems most connected to the original junction. The searching behavior of turtle ants reflects the highly modular distribution of their food resources, for example, in nectar from flowers that grow on clusters of branches at the sunny outer edge of the canopy. Because the ants tend to search branches extending from the nearest junction, when they find one food source, such as a flower with nectar, they are likely to find more on connected branches.

In an unstable environment where activity is easy, with resources clustered in time and space, many aspects of the turtle ants' collective behavior provide the capacity to adjust rapidly and locally to changing conditions: reliance on local regulation using interactions at each junction to determine the shape of the trails, combined with modular search, and a feedback regime in which the default is for the trail to keep going unless inhibited.

In summary, harvester ants regulate foraging using a system in which interactions adjust slowly, the feedback is positive reflecting a default set not to be active unless stimulated, and the modularity is low. All of these are consistent with a stable environment, in which there is a high cost in water to obtain water and food, and the distribution of resources is scattered, so that there can be a slow spread of information among all the foragers. In contrast, turtle ants use a system in which interactions adjust rapidly to changing conditions, the feedback is negative, reflecting a default set to keep activity going unless inhibited, and the modularity is high. These dynamics are consistent with an unstable environment, in which activity is easy, and the distribution of resources is clustered in space and time.

More generally, ants provide many examples of diverse ways that collective behavior can operate in relation with changing environments. There are more than 15,000 species of ants, with species in every terrestrial habitat except for polar regions. In previous work (Gordon, 2019), I considered how the collective behavior of ants suggests trends in how collective behavior operates in relation with changing surroundings. These trends may be reflected in other systems.

There are many familiar examples of collective behavior, and of their flexible response to conditions. Perhaps the most familiar are from spatial patterns, as when bird flocks (Ling et al., 2019), fish schools (Herbert-Read et al., 2017), or even fruit flies (Ferreira & Moita, 2020) adjust their spatial pattern in response to predators. Similarly, the migration of groups of cells, such as the movement of neural crest cells in mammalian embryos, is a response to signals from contact with other types of cells (Mayor & Etienne-Manneville, 2016).

The interactions that produce collective behavior use an enormous variety of mechanisms, for example, visual in the case of birds (e.g., Ling et al., 2019), and tactile and chemical for cells. Another general form of collective behavior is task allocation in an ant colony or vertebrate social group, which determines which individual is currently performing which task, or differentiation in an embryo, which determines which cell currently has which function. These also work through interactions, olfactory in the case of ants, or chemical and tactile for the cells in an embryo.

The comparison of the collective behavior of harvester ants and turtle ants, outlined above, illustrates hypotheses about general trends in the correspondence between how interactions work and the dynamics of the surroundings (Gordon, 2014, 2016, 2023). To characterize how surroundings change, I consider three gradients, all familiar in ecology. The first gradient is in stability, how frequently and how much the surroundings change, ranging from very stable with rare or little change, and few threats, to unstable with frequent or large changes and high risk. The stability of the surroundings shapes natural systems; for example, stability in resources shapes the diversity of ecological communities (May, 2019), and many physiological processes, such as plant growth rates (Grime, 1974) reflect a response to threats or disturbance. The second gradient is in energy flow, what the surroundings require the system to use, relative to what it obtains, ranging from a system where what is used is large relative to what is obtained, to the opposite, where what is used is small relative to what is obtained. For example, harvester ants must lose water to evaporation to obtain water and food, while turtle ants, foraging in a humid environment, can obtain food and water with much less water loss. Changing conditions set up the balance of energy flow; this can be traced at many levels of natural systems, from biochemical processes (Morowitz, 2012) to foraging behavior (Charnov, 1976). The third gradient is in the distribution in space and time of resources and demands on the system, ranging from scattered, homogenous, or random to clustered, patchy and ephemeral (e.g., Maurer, 1990).

Drawing on ideas from dynamical systems (Adler, 2005; Ferrell, 2022) and network science (Newman, 2018), I will consider three dynamical features of the interactions that regulate collective behavior: the rate at which interactions adjust to changing condition, the feedback regime triggers and inhibits the behavior, and the modularity of the interaction network.

The first hypothesis for a correspondence of the dynamics of behavior and its surroundings is about rate: how rapidly interactions are used to adjust to changing conditions is associated with the stability of the

surroundings and the distribution of resources and demands. Systems that need to respond to rapid change are likely to use interactions that adjust rapidly to conditions. For example, ant species that exploit ephemeral and patchy resources, and that face competition with other species, regulate foraging through rapidly deposited and rapidly evaporating pheromones (Deneubourg et al., 1986). Similarly, the response of skin cells to close a wound, a rare but risky event, is very rapid. (Galcko & Krasnow, 2004). By contrast, slow change is possible in very stable environments; examples are the pruning of neural connections in brains (Navlakha et al., 2018); the slow growth of hair cells in mammals, which evolved in response to seasonal changes in temperature (Amoh et al., 2009), or the slow changes in branch shape of trees growing around an obstacle (Groover, 2016).

A second hypothesis is that the feedback regime that uses interactions to activate and inhibit activity is likely to reflect the energy flow required to operate in the environment. A system can combine different forms of feedback that work together to regulate it. A suite or network of feedback loops is a feedback regime (Ferrell, 2022), consisting of the linked processes that stimulate and inhibit activity, such as a signaling pathway in a cell or a set of relationships in a social group. Collective behavior that is risky is likely to have the default set at inactivity, and require positive feedback to be initiated, such as plant flowering in response to seasonal changes of temperature (Whittaker & Dean, 2017) or, I'd suggest, fast-forward loops in gene transcription (Gordon, 2014). By contrast, when an activity is not risky, or the ratio of energy expended to energy gained is low, the default may be set to keep going, and feedback can inhibit the system only in response to some negative event. For example, young plants keep growing toward light unless they experience too much light (Lopez-Juez, 2009).

A third hypothesis is that high modularity in the interactions among individual components of a system is likely in unstable or risky environments when local action is needed. The modularity of interactions influences how quickly and how locally the system responds (Wagner et al., 2007). For example, many desert plants have a modular structure that allows some parts of the plant to die when resources are scarce, but other modules can survive (Salguero-Gómez & Casper, 2011). The parallel hypothesis is that low modularity, with connections distributed across the system, is likely in a stable situation, allowing for a slower and more thorough spread of information. For example, it seems that the network of connections among neurons used in cognition are more modular than those used in perception (Bassett & Bullmore, 2017).

The hypotheses I propose here suggest that to learn how interactions shape collective outcomes in a particular system, we can look at how the surroundings change, and consider how the system is likely to work. Do conditions change rapidly or slowly, and does the system adjust accordingly? Is the outcome associated with high risk? If so, is the default to remain inactive unless triggered by some feedback related to current conditions? If not, is the default to keep going unless inhibited? Does the system need to respond locally to change or does it need to broadcast a response throughout the system? This can indicate how the network of interactions is likely to be structured, whether all the participants are equally linked or instead whether the interactions are clustered in modules.

The proposal that collective behavior evolves to respond to changing surroundings draws on a large and varied tapestry of ideas in evolutionary biology that I will not attempt to review here. One important theme is the large body of work that examines both theoretically and empirically the evolution of phenotypic plasticity, beginning with Levins' *Evolution in Changing Environments* (1968). A second is the "extended synthesis," based on the premise that organism and the environment influence each other (Laland et al., 2014). A third is the evo-devo approach to developmental biology that sees evolutionary innovation as a response to changing conditions (West-Eberhard, 2003).

A basic premise of this approach is that the relation of inside and outside, organism and environment, is dynamic, because everything changes (Nicholson & Dupré, 2018) and systems change in response. Even the absence of change is the result of regulation to deal with changing conditions. The study of evolution, development, phenotypic plasticity, and behavior all explicitly seek to explain change. To do this is to abandon the illusion that individuals are driven by inherent and fixed properties that are independent of their surroundings. It would not be possible to review here all of the recent work in biology that seeks to bring inside and outside together to explain how the system changes. (Sultan [2015] is a good place to start). All have in common the insight that the relation of inside and outside goes in both directions, that all natural entities influence what is around them, while what is around them influences what they do. Everything alive is responding to other living entities and to changing conditions which they in turn modify.

This insight has led to a shift in thinking about innovation over the course of evolution. If each component simply carries out the instructions of its genes, then random mutation is needed to lead to new behavior of the components. But if systems are working collectively

to respond to changing conditions, then innovation is in the coordination of the interactions that lead to collective outcomes, rather than in the properties of the component parts (West-Eberhard, 2003). These interactions occur at every level, including gene transcription networks that regulate gene expression in response to conditions, or the pattern of antennal contacts that stimulate ants to forage. It seems likely that the evolution of all forms of collective behavior is shaped by how the collective outcome functions in changing conditions. Since innovation over the course of evolution arises from responses to conditions, it seems plausible that similar responses are likely to arise in conditions that change in similar ways. Another argument for why such patterns are likely is based on adaptation; a similar solution can work well for different systems that are solving the same problem. This would lead to trends in how collective behavior is regulated, using interactions to adjust collective outcomes.

As in other fields of biology, the approach described here to investigating how collective behavior works focuses questions on the dynamic relations among entities and their surroundings rather than on the internal causes of behavior. For example, what causes a harvester ant forager to leave the nest on its next trip? The processes inside the ant, including circadian rhythms of gene expression (Ingram et al., 2016) and the action among its brain cells of neurotransmitters such as dopamine (Friedman et al., 2020), are influenced by its interactions with other ants and with current conditions, which in turn changes what they do. Patterns in the dynamics of foraging show variation among colonies. Colonies differ in how they regulate foraging in response to day-to-day changes in food availability and humidity (Gordon et al., 2011; Pagliara et al., 2018) because the foragers of one colony differ from those of another in how humidity influences their decisions to leave the nest in response to interactions with returning foragers. Natural selection is shaping the variation among colonies (Gordon, 2013). Selection pressures may be shifting in response to climate change and the associated drought (Sundaram et al., 2022).

These hypotheses are intended to raise empirical questions about collective behavior in relation with its surroundings. This moves beyond an approach that treats a natural system as composed of entities whose internal properties determine what they do. From that perspective, an embryo is made up of cells that follow instructions in their genes; an ant colony is made up of individuals each carrying out their own strategy, and so on. Such an approach seeks to explain how a system works using the properties of its component parts. But this does not fit what we observe. We see that systems are not broken up into parts, and that what they do is not a

simple consequence of internal properties of those parts, but also reflects how the parts function together in their surroundings.

The idea of agency helps in finding ways to ask how a system changes in relation to what is around it, and to explain how the parts of the system interact to generate its behavior. First, attributing agency to a system unites it, making it possible to talk about it as an entity in relation with its surroundings. The idea of “collective behavior” serves a similar purpose. The body shape and size of an organism is the outcome of collective behavior among cells in development; the splitting and fusion of a flock of starlings is the outcome of collective behavior among the birds. An emphasis on the dynamics of collective behavior, situated in changing surroundings, is also linked to the idea of agency. One way to ask how a natural system operates collectively in relation to its environment is to ask what objectives it achieves. The ant colony acts in a way that satisfies certain objectives, while no ant makes any global assessment of the number or type of junctions being used. As Denis Walsh has pointed out, in explaining collective behavior, we could talk about the agency of the individuals or of the collective (Walsh, 2016). That is, each ant in the trail has agency, following a gradient of pheromone, putting down more pheromone itself, and performing tasks such as collecting nectar. The colony also has agency in maintaining and repairing the trail and determining its configuration.

For example, we asked how a turtle ant colony's trail networks meet three objectives: finding the shortest path in distance traveled, finding the shortest path in number of junctions, or finding the path through a junction most easily reinforced by pheromone so most likely to take ants to the same edge beyond the junction (Chandrasekhar et al., 2021). To do this, we mapped the vegetation along the paths used by the ants, and also mapped the surrounding vegetation up to five junctions away from every junction along the trail. To measure the distance traveled, we measured the length of each branch or stem between each pair of junctions. We counted the number of junctions in the path used by the ants. Finally, we evaluated which paths through a junction were mostly likely to be reinforced. Ants of this species have very short antennae and so cannot detect pheromone deposited far away, so if an ant uses a path through a junction that is different from the one used by the ant before it, it is unlikely to detect the pheromone deposited by the previous ant (Chandrasekhar et al., 2021). We used the configuration of the branches and vines in each junction to assign an index corresponding to the probability that successive ants would take the same path through the junction, thus directing the next ant to

the same path beyond the junction. The index was based on observation of ants traveling across junctions and choosing a particular path at the far end of the junction. At a simple fork in a branch, every ant is likely to go the same way, thus reinforcing the path through the junction. But a junction with many vines or branches offers many possible ways that an ant could cross it, so each ant may go a slightly different way. When ants take different paths along the curves and knots of vines that form some of the junctions, one ant will not detect the pheromone put down by the last one, and may choose a different path beyond the junction.

We then compared the paths the ants actually took with those of simulated, random paths through the same vegetation. We asked how well the observed paths, compared to the random ones, met the three objectives, taking the shortest path in distance traveled, or in number of junctions, or using the junctions most likely to be reinforced by pheromone. We found that the paths meet two of the objectives but not the third. Compared to random paths through the same vegetation, the paths are more likely to use the junctions most easily reinforced, and to minimize the number of junctions, but not to minimize the distance traveled. Because each junction is an opportunity for ants to get lost, taking the paths most easily reinforced and minimizing the number of junctions both contribute to the coherence of the trail.

Thus in the collective process that regulates the trail networks of turtle ants, keeping the ants together on the trail is prioritized over finding the shortest path (Chandrasekhar et al., 2021). (This is consistent with a humid environment in which activity is easy.) Specifying what objectives are met by the ants is a way to describe how the colony's behavior is embedded in the conditions it deals with. In this sense, the collective behavior of the colony draws on the agency of the ants and manifests the agency of the colony. “Collective behavior” or “agency” does not attribute to the system any inherent property that supposedly causes its behavior. Just as an embryo does not have an essence that acts as an agent, an ant colony does not have a mind. Both the individuals and the collective adjust to changing conditions to produce trail networks that meet functional objectives.

A focus on collective behavior or agency emphasizes a common theme across different fields of biology. The biologists who study systems of very small things, such as cells, can manipulate the system so as to identify the participants in collective behavior and the feedback that links them. By contrast, biologists who study systems of large things, such as plants and animals, can observe how surroundings change and how the system responds. These complementary perspectives come together in investigating the collective behavior of any natural

system by considering how it works in relation with its surroundings. The goal is not to find a core or master that controls the rest. Instead, the project is to understand, at each layer, the relation of the participants and their surroundings and how that changes to adjust to the current situation.

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There are no data reported in this manuscript.

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