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The Ecology of Collective Behavior in Ants

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Abstract

Nest choice in *Temnothorax* spp.; task allocation and the regulation of activity in *Pheidole dentata*, *Pogonomyrmex barbatus*, and *Atta* spp.; and trail networks in *Monomorium pharaonis* and *Cephalotes goniodontus* all provide examples of correspondences between the dynamics of the environment and the dynamics of collective behavior. Some important aspects of the dynamics of the environment include stability, the threat of rupture or disturbance, the ratio of inflow and outflow of resources or energy, and the distribution of resources. These correspond to the dynamics of collective behavior, including the extent of amplification, how feedback instigates and inhibits activity, and the extent to which the interactions that provide the information to regulate behavior are local or spatially centralized.

INTRODUCTION

Ants work collectively to perform many tasks, such as to collect, process, and distribute resources and to find, build, and defend their nests. Their collective behavior is the result of interactions among individuals. To explain how collective behavior operates, we formulate a model or algorithm that specifies how individuals respond to interactions and how this produces the collective outcome. One familiar example is the algorithm that describes how ants deposit and respond to trail pheromone so as to generate a foraging trail (24).

The diversity of collective behavior in ants (69) arises from the same evolutionary trajectories that produced the staggering diversity of morphology and resource use. About 14,000 species of ants have been identified, and all have in common that they live in colonies, consisting of some arrangement of sterile female workers and reproductives. Although only about 50 species have been studied in detail, it is already clear that ant species differ greatly in ecology and in behavior.

Collective behavior, like any phenotypic trait, evolves in relation with a dynamic environment. Here I consider some aspects of the dynamics of the environment that may be important in the evolution of collective behavior in ants (57). The first is stability, the frequency of change in the conditions associated with that behavior. For example, how quickly a colony chooses a new nest site, and moves to it, is probably related to how long the new site will be available. This first feature of the dynamics of the environment is related to a second, the threat of rupture or disturbance—both how likely disruption is and how much is at risk if it occurs. For example, red wood ant colonies, living in a very stable environment, establish very permanent trails from nests to trees that persist for years (34); turtle ant foragers forage in vegetation that is often disturbed or ruptured, and they easily and frequently create new trails (55, 59). A third is the ratio of intake and outflow, in energy or another resource—that is, the relation between how much the behavior brings in and how much is used to accomplish it. For example, for harvester ant colonies in the desert, this ratio is low, because foraging ants can easily lose more water to desiccation while searching for food than they can obtain by metabolizing the water from the fats in the seeds they collect. A fourth is the distribution of resources in time and space—for example, whether the distribution is patchy or scattered (27, 68, 104).

A growing number of studies show that collective behavior in ants is related to environmental conditions. Species differences in behavior, such as foraging trail networks (87) and other foraging behavior (80), the location of waste heaps (37), task flexibility (7), and defensive behavior (43), all reflect ecological factors such as climate, resource distribution, risk of infection, or desiccation risk. Species differences in collective behavior also reflect differences in physiology related to ecological conditions; an example is desiccation resistance (14).

In general, the dynamics of collective behavior are likely to correspond to the environment in which the behavior functions (**Figure 1**). One important aspect of the dynamics of collective behavior is how it amplifies. For example, trail pheromone creates a form of positive feedback that rapidly amplifies the number of ants on the trail (42). One ant lays pheromone, the next ant interacts with the first by detecting the pheromone deposited, and then it puts down pheromone in turn. In the aggregate, both the numbers of ants and the amount of pheromone increase or are amplified. Amplification is related to a second feature: how the feedback generated by interactions makes it easy or difficult to instigate the behavior. If positive feedback is required, then the default is not to start until the positive feedback occurs. For example, a harvester ant colony does not begin to forage unless foragers interact with returning patrollers at a high enough rate (65); the default is to not forage unless activated. By contrast, when feedback is negative, the default is to keep going unless something negative occurs. For example, Argentine ant workers persistently explore new spaces (54) even if there are obstacles; more drastic negative feedback is required to inhibit search. A third important feature of the dynamics of collective behavior is how information
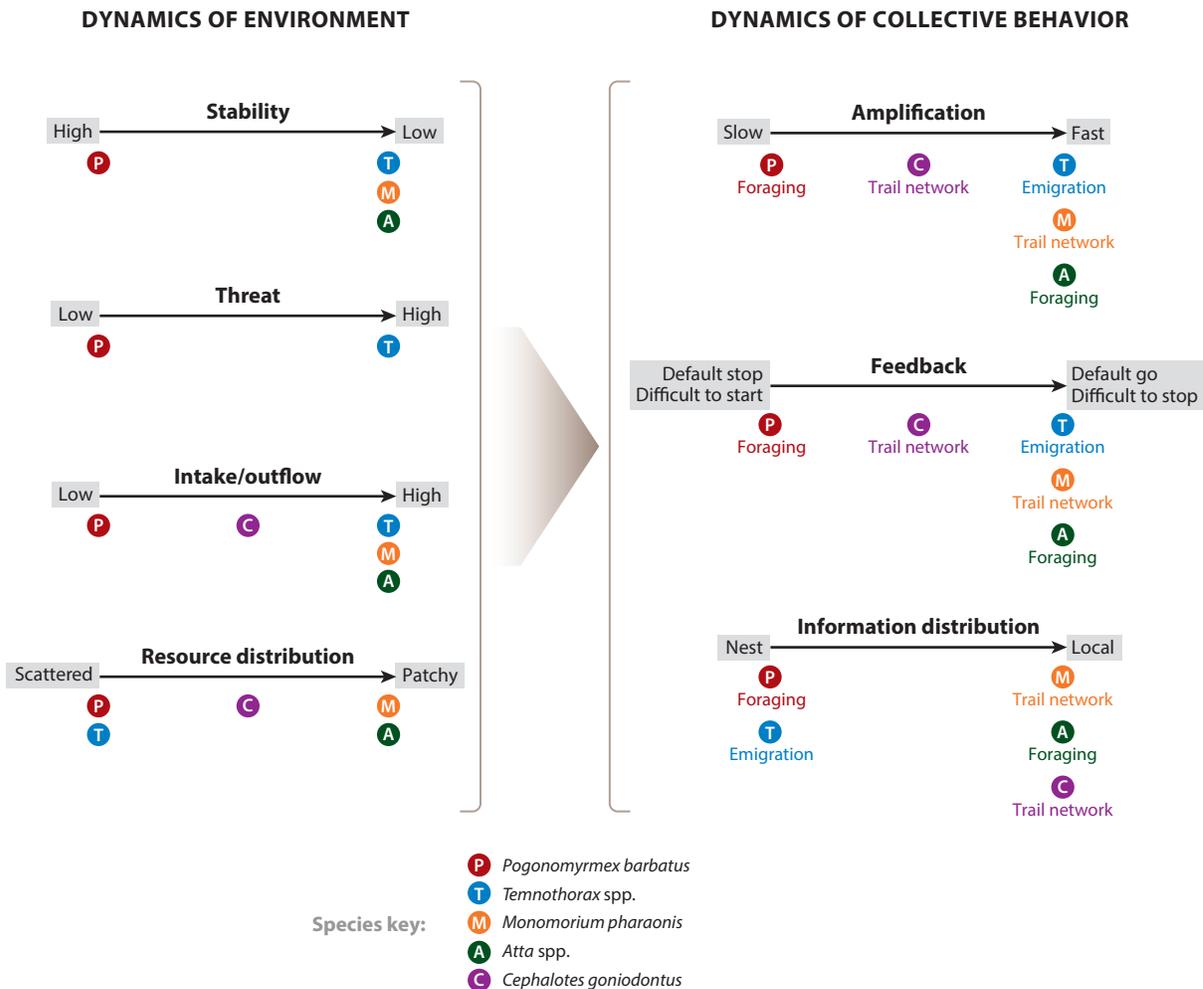
DYNAMICS OF ENVIRONMENT

DYNAMICS OF COLLECTIVE BEHAVIOR

Figure 1

Correspondences between the dynamics of environment and the dynamics of collective behavior. The left panel shows gradients in features of the dynamics of a colony's environment: stability, threat of disturbance, the ratio of intake to outflow of energy or resources, and resource distribution. The right panel shows gradients in features of the dynamics of a colony's collective behavior: amplification (e.g., in numbers of ants at a resource); feedback (e.g., whether a stimulus acts to instigate or stop the behavior); and how information is regulated spatially (e.g., whether the interactions that regulate behavior take place at a central location such as a nest). The species discussed in the text are shown with colored symbols (see key in the figure). Environmental conditions shown on the left are associated with the behavior shown on the right. For example, for the desert seed-eating ant *Pogonomyrmex barbatus*, environmental conditions, including high stability, low threat, a low ratio of intake to outflow in resources, and scattered resources, are associated with slow amplification, feedback that sets the default as inactivity, and centralized interactions in the regulation of foraging activity.

is regulated spatially, whether the behavior is regulated through local interactions or at a location that is distant such as a nest. Local regulation can be faster than the use of spatially centralized information (87) because of the lag introduced by the time it takes to get back and forth from a distant or central location. For example, Argentine ants recruit from food sources directly from the trail, rather than from the nest, which allows for faster recruitment than if ants had to go back to the nest to summon more foragers there (40).

Modeling collective behavior is an exciting new field. For the study of ants, it is progressing faster than behavioral ecology, and, as a result, there are currently few ant species for which both the collective behavior has been modeled and the ecology has been investigated. Thus many of the ecological features described here have not been studied in detail. I hope that the suggestions I make here will stimulate further research. I consider three kinds of collective behavior: first, nest choice in species of *Temnothorax* ants that emigrate frequently from one nest to another; second, task allocation, including task switching in *Pheidole dentata*, *Temnothorax rugatulus*, and *Pogonomyrmex barbatus*, and the regulation of activity in foragers of the leafcutter ants in the genus *Atta* (mostly *Atta colombica*) and the harvester ant *P. barbatus*; and third, trail networks in the pharaoh ant, *Monomorium pharaonis*, and the turtle ant *Cephalotes goniodontus*. I use these examples to suggest correspondences between the dynamics of collective behavior and of the environment in which it functions (**Figure 1**).

NEST EMIGRATION

Nest emigration has been intensively studied in several species of *Temnothorax* ants, mostly *T. curvispinosus*, *T. albipennis*, and *T. rugatulus*, which nest in temporary spaces such as acorns or cracks in rocks and move frequently (87, 91). A long series of ingenious laboratory experiments have examined what the criteria for nest choice are, and how the choice of a new nest and subsequent emigration are organized collectively (83, 106)

All *Temnothorax* species studied have a similar basic algorithm for nest choice and emigration that have certain features in common (45, 105, 107). If conditions in the nest are unfavorable, scouts inspect and assess the quality of possible nest sites. On the basis of that assessment, a scout either goes back to the nest and starts tandem recruitment for more scouts or continues searching. Eventually, they begin to transport ants to the new nest, depending on the rate of antennal contact with nestmates at the new site to estimate density. When a threshold density or so-called quorum is reached, the ants at the new nest site go back to the home nest and recruit other ants to the new one. In some species, the decision to choose a particular nest is also influenced by pheromone cues (114).

The algorithm that regulates nest choice and emigration in *Temnothorax* (107) seems to give priority to escaping the current nest rather than finding a better one. The first line of evidence for this is that nest choice is easily swayed. Not all colonies go to the best site; in laboratory experiments, there is a tendency to choose a higher-quality site, but it is never the case that all colonies choose it. The quality of nests chosen varies, at least in part, because many factors can influence nest choice. These factors include differences among individuals in decision criteria (29, 98, 114) and the effects of current conditions such as where ants have previously found food (16), the location of the queen (28), recent foraging locations (120), and frequency of disturbance (89). The second line of evidence is that emigration is easily initiated and difficult to stop, favoring moving somewhere over not moving at all. For example, the larger the colony, the more ants participate in the scouting and recruitment process, so the faster emigration proceeds (44). Moreover, the process that leads to nest choice and emigration is easily amplified when ants at the new site begin to use the rate of contact to assess density, and to recruit others, instead of one-on-one recruitment through tandem running (105).

Figure 1 shows the conditions that characterize the environment of *Temnothorax* colonies with respect to nest choice. It seems that *Temnothorax* spp. tend to live in unstable environments. Apparently, the energy spent in moving is low, so that a new nest brings in more resources than are lost moving to it. The threat and costs of danger in the nest are high, due, for example, to a broken nest cavity or the risk of parasitism (76). Nest sites are often a scattered rather than patchy resource on the small spatial scale on which colonies move (e.g., 41).

Species of *Temnothorax*, and populations within these species, vary in nest choice and emigration. Further work is needed to learn whether this variation reflects differences in the basic algorithm used for nest choice or instead tuning of the threshold values of the parameters (107). One possible source of tuning is the extent to which individual assessment and density at nest sites each contribute to the collective decision. When more input is based on individual assessment relative to assessment of density, nest choice is likely to be slower and colonies may choose higher quality nests.

It is clear that variation in the nest choice behavior of *Temnothorax* is associated with ecological factors that affect the need to emigrate, such as parasite pressure (76). There seems to be selection on variation among colonies in the propensity to emigrate (116). Many observations suggest that when nest sites are scarce (5, 70), standards of nest quality and the threshold density needed to move may be lower, as colonies have to take whatever sites are available. Increases in nest site abundance stimulate emigration and budding (41). Populations within species vary in collective behavior in response to changing conditions related to the costs of emigration and nest site availability (90). For example, colonies of *T. rugatulus* in warmer conditions are more likely to explore than colonies in colder conditions (117) and are more likely to engage in exploratory behavior and aggression when competition for resources and nest sites is high (5).

Unlike the algorithms that regulate emigration in *Temnothorax*, the process that regulates emigration in some other ant species appears to give higher priority to choosing a better nest than to escaping the current one. For example, in the harvester ant *P. barbatus*, about 20% of colonies attempt to move nests each year, but only, at most, 10% actually move (52). The energy demands of emigration are high, because it is very difficult to excavate a new nest in the hard desert soil, and moving from one to another takes many hours and risks both desiccation and predation. The environment is stable, and disasters that affect nests, such as flooding, are very rare. Nest sites are difficult to find; sometimes, colonies move into nests of neighboring colonies that died. As a consequence, most colonies stay in the same nest for the 20–30-year life span of the colony (73). Perhaps a very high threshold of interaction between the ants that build the new nest and other ants back at the nest is required to instigate a move. By contrast, the harvester ant *Messor andrei*, which nests in looser soil, moves frequently. Remarkably, in *M. andrei*, different colonies move in and out of the same nests, and as nest configuration influences activity outside the nest (102), it may be that nest configuration also influences the regulation of emigration.

TASK ALLOCATION

Task allocation, the process that determines which individual performs which task, and when that individual is active, is the most extensively modeled aspect of collective behavior in social insects (58). Such models predict an individual's activity as a consequence of its interactions with others (60), of aspects of the environment related to a task, such as forager response to food availability (64), or both (99). Some excellent reviews of these models include References 6, 78, 79, and 97. How task allocation can work without central control is a general question about any process that involves many agents and more than one task. In fact, a recent literature search for "task allocation" led me to more articles about computer science, robotics, and operations research than to studies of social insects.

Many models of task allocation postulate a threshold: After a certain number or rate of interactions, or exposure to some stimulus, a change in behavior becomes likely. The response threshold can be modulated in many ways, from a deterministic cutoff point (6) to accumulated evidence as in a leaky integrator model (23, 108, 115). Models also differ in what constitutes the interactions that regulate collective behavior. Most are olfactory [though tactile cues may also be important

(111)], including antennal contact, in which one ant perceives the cuticular hydrocarbon profile of another (65), or the transfer of a pheromone or hormone (reviewed in 6).

Models of task allocation differ in the extent to which individual identity is specified. If any ant is equivalent to any other ant performing the same task, or of the same activity level, then the process of task allocation can be viewed as a parallel distributed process as in a Hopfield net or neural network (60, 88, 108). If instead each individual is identified, so that it is possible to track which one interacts with which other, then the process can be viewed as a network, and its dynamics are modeled accordingly (84, 103, 123).

Task allocation includes two distinct processes (58). One is task switching, the process that moves an ant from one task to another. The second is the process that regulates the activity of ants in a particular task group. That is, what determines whether an ant is a forager today, or this week, is a different process from the one that determines whether the ant is foraging right now.

Task Switching

Despite the many models of task allocation in the literature, surprisingly little is known about the extent to which, in a particular species, task switching depends on interaction among workers and on direct assessment of what needs to be done. Thus there are few species of ants for which the algorithms for task switching can be specified. In the harvester ant *P. barbatus*, as in other species (8), task groups differ in cuticular hydrocarbon profile (122). In the course of a brief antennal contact, an ant perceives the cuticular hydrocarbon profile of another (65). The rate at which an ant meets ants of a particular task group is a cue to the current rate at which that task is performed. The rate of antennal contact can thus provide feedback that influences task switching and the transition between activity and inactivity. For example, ants of *P. barbatus* that meet midden workers at a high rate are likely to switch tasks to midden work (62).

Some studies of task switching suggest that the process that leads to switching between tasks, and between activity in some task and complete inactivity—that is, not doing any task at all—is likely to be associated with the stability of the environment. In *P. barbatus*, in an environment where disturbances are rare, ants usually stay in the same task group from day to day, and task switching occurs in response to unusual situations that require more ants in a particular task (50). Experiments with marked ants (50) show that most task switching is within the group of ants currently active outside the nest, who do not mix with the inactive ants deeper in the nest (1, 51), as in other *Pogonomyrmex* species (82). By contrast, workers of *Temnothorax rugatulus*, who are often called upon to respond to drastic changes, such as a move to a new nest, more easily switch tasks (18, 81) and make transitions between actively performing some task and being mostly inactive, not performing any task (18, 103).

An important influence on task switching is age polyethism; workers tend to move from tasks inside the nest, such as brood care, to tasks outside the nest, such as foraging, as they grow older (e.g., 15, 50). The neuroanatomy and neurochemistry of age polyethism has been extensively studied in *Pheidole dentata* (47, 48, 64, 72, 77, 94, 95). Biogenic amine expression and brain morphology change dramatically during the first few weeks of a minor worker's life (92). In this species, as in many other *Pheidole* species, minors perform a variety of tasks, and when needed, majors will switch to perform those usually done by minors. Minor workers continue to do brood care even after they begin to work outside the nest (118). As a minor worker matures over the first 10 days as an adult, there are changes in brain anatomy and serotonin titer that are independent of experience (93). However, little is known about what stimulates individuals to change tasks.

The enormous ecological diversity of *Pheidole* (85) provides an opportunity to examine the relation between task switching and ecology and to trace the evolution of task allocation using

phylogenetic studies (92). *Pheidole* species differences in task flexibility or task efficiency are not correlated with morphological specialization (86). While some differences among species in the behavior of majors might be due to sampling effects, because species differ in the proportion of workers that are majors (119), some may be associated with ecological factors. For example, colonies of *P. dentata* respond to intrusions by the invasive fire ant *Solenopsis invicta* by retreating and moving (125), although eventually majors will switch to join in defense (75); similarly, in response to attack by phorid flies, majors run away or stop foraging (39). By contrast, in *P. pallidula*, colonies respond to threat on a longer timescale by producing more majors (100) that fight intruders. This may be because *P. pallidula*, an opportunistic forager among many competing species (25, 26), faces more long-lasting threats than *P. dentata*, which nests in forest communities with few competitors.

Patterns of brain development as ants move from one task to another are associated with species differences in ecology. For example, brain development that depends on prior experience may function best when stable conditions lead to stable brood production, so that there is a steady flow of ants from one task to the next, with older ones available while the younger ones try out the task (93). Brain development of adult workers depends on task experience in *Pseudomyrmex spinicola* (2), while in *Pheidole dentata*, the brain development of young minor workers is not affected by their experience with brood care (93). This may reflect differences between *Pheidole* and *Pseudomyrmex* in the stability of brood production. *Pseudomyrmex spinicola* is a tropical, arboreal plant mutualist, nesting in acacia thorns. Brood production for *Pseudomyrmex* in the tropics may be more steady than that of *P. dentata* in the temperate zone, because of the reduced seasonality of the tropics and because colony growth in ants that are plant mutualists is linked to the long-term growth of the plant hosts (46).

Regulation of Activity

A second feature of task allocation is the moment-to-moment regulation of activity in a particular task. The regulation of foraging activity is well studied in leaf-cutter ants, which collect leaves to feed the fungus that the colony eats. Both the rate of foraging and what is collected are regulated locally, on the trail (30, 92, 112) [although the rejection of leaf material toxic to the fungus is coordinated at the nest (3)]. Foragers on the trail adjust their behavior in response to many kinds of encounters. In *A. colombica*, when ants on the trail are attacked by parasitic phorid flies, other foragers move faster (20). When an obstacle above the trail requires ants to bring in smaller pieces of leaves, forager rate increases, which helps to compensate (31). At the same time, workers without leaves work to remove the obstacle, which allows faster transport (12). Foragers shift between cutting leaves and carrying them, depending on the rate at which they encounter dropped pieces of leaves left on the trail [transport chains (112)].

The rate at which ants travel on the trail is also influenced by the rate of antennal contact between inbound and outbound foragers (10, 31, 35). In turn, the rate of contact depends on crowding and trail width (11). Traffic moves in lanes to regulate the rate of contact at branching points (19, 38). In *A. cephalotes*, and perhaps in other *Atta* species, encounters on the trail help to guide the outbound foragers to particular food sources that returning ants are bringing back (35). This process helps regulate the extent to which ants strip a tree of leaves and leads foragers to change to trees where more leaves are available (126). Foragers that return to the nest without leaves cluster together, reducing the probability that they engage outgoing workers in encounters that will not provide any information about the current food sources (32).

Overall, the regulation of foraging in *Atta* colonies is rapid on the basis of local interactions on the trail. This allows colonies easily to amplify the rate at which different patches of resources

are found and collected. Feedback based on many kinds of encounters makes foraging difficult to stop; the default is to keep going. The dynamics of foraging in *Atta* are consistent with their ecology (**Figure 1**). Many species forage in tropical forests in an unstable environment: They encounter many other ant species as well as other insects, face frequent disturbance by many animals, and move through complicated vegetation (96). Rapid adjustment of foraging is needed because foragers collect leaves to feed a fungus that is prone to rapid declines due to toxins, bacterial attack (22), and other changes in condition that can occur on the timescale of hours and weeks. It seems that for leaf-cutter ants, the flow of energy for foraging brings in more, in food, than is spent; in fact, it has not been shown that ants save energy by bringing in the largest leaf fragments possible. Instead, the regulation of foraging seems based on having plenty of ants available to forage, with many features that get the most ants to the food as soon as possible.

The species of *Atta* that have been studied most, *A. vollenweideri*, *A. cephalotes, and A. colombica*, seem to be similar in how they use interactions on the trail to regulate current forager activity. But there is considerable ecological diversity among *Atta* species, in habitat, colony size, and associations with fungi and other microbes (126). There are likely to be differences among species in the algorithms for the collective regulation of foraging activity that reflect differences in ecological conditions.

By contrast, with leaf-cutter ants, foraging activity in the harvester ant *P. barbatus* is regulated more slowly by interactions inside the nest. An outgoing forager decides whether to leave the nest on its next trip using the rate at which it meets foragers returning with food (61, 66, 101). The algorithm for this decision is based on how each ant assesses its recent experience with returning foragers. Assessment of interaction rate uses a leaky integrator process (23), analogous to the process used by a neuron to accumulate the stimuli that prompt it to fire. Each interaction stimulates foraging, but that stimulation decays, so the decision to leave the nest to forage depends on the accumulated effects of many interactions. This allows the ant to respond to the rate of interaction without counting or evaluating rate directly. This feedback links the rate of foraging to food availability: the more food is available, the faster ants find it and the more quickly they return to the nest, stimulating others to leave.

Harvester ants forage in a stable environment of open ground in desert grasslands with few threats except predation by horned lizards. The ratio of intake to outflow of water is low: Colonies must spend water to obtain water. A forager loses water out searching in the sun, and ants obtain water from metabolizing the fats from the seeds they eat. Water limitation is ecologically important: Colonies that conserve water by reducing foraging in hot conditions show higher reproductive success in offspring colonies (56). The distribution of seeds is scattered, not patchy; seeds are distributed by wind and flooding, and seed distribution changes quite slowly, on the scale of weeks and months (53).

The collective regulation of foraging in harvester ants reflects the dynamics of the desert environment (**Figure 1**). Foraging is not easily amplified. Because the regulation of foraging relies on spatially centralized information through interactions at the nest, the rate at which foraging rates can change is set by the duration of a foraging trip, about 20 minutes (1), and foragers do not recruit to newly discovered patchy resources (49); recruitment takes place only if a patch of food, which is very unusual, is provided early in the morning, before foraging begins, when patrollers are active. Foraging is not easily initiated, requiring a long process involving the rate of return of patrollers (65); if this does not happen, the colony does not forage. Foraging is easy to shut down; for example, when many ants are removed, as they sometimes are by their main predator, the horned lizard, the rate at which ants leave the nest slows down (61). Thus the feedback for this system sets the default at not foraging, and positive stimulation, in the form of returning foragers with food, is required to elicit foraging.

The harvester ant system, which minimizes forager trips, contrasts with that of leaf-cutter ant colonies, which is regulated to deploy many ants as quickly as possible. Leaf-cutter ant colonies are two orders of magnitude larger than harvester ant colonies. A mature colony of the harvester ant *P. barbatus* has 10,000–12,000 workers (51) and up to about 1,500 foragers that might bring in 3,000–4,000 food items in a day (1); a mature *A. colombica* colony has 1–2.5 million workers, bringing in up to 100,000–350,000 leaf fragments per day per colony (126).

TRAIL NETWORKS

Many species of ants create networks of foraging trails (87). Perhaps the most intensively studied species is the pharaoh ant, *M. pharaonis*, an invasive species now distributed worldwide, with large colonies that bud easily (13) and compete strongly with other species (43).

The trail networks of *M. pharaonis* connect nests and food sources. Trail networks are easily established, and they are difficult to inhibit while the food source lasts. They provide the classic example of rapid amplification of foraging rates (42), using an elaborate system of pheromones to form trails. Recruitment is local, with new trails easily formed from old ones.

The algorithm that regulates the trail networks in *M. pharaonis* seems to prioritize recruitment, leading to the rapid amplification of numbers of ants at food sources. This rapid recruitment allows them to choose among available food sources without comparing them directly, merely by choosing the strongest trail (121). Decentralized recruitment from the trail rather than the nest allows for faster response to new food sources, as in other opportunistic species (40).

Many features of the regulation of trail networks in *M. pharaonis* serve to maintain the pool of ants available for recruitment to a new food source once a previous source is depleted. In this species, the amplification process to form new trails requires large numbers of ants; trails do not form if there are not enough ants to lay a trail before the volatile pheromone decays (4). The pool of available recruits is replenished in two ways. First, network structure is used to funnel ants back to be available to be recruited. The trail networks have a tree-like shape: The main trunks come from the nest, other trails branch from the trunk, others from branches, and so on. The angles between branches and trunks determine path length and amount of ground covered (as in leaf-cutter ant networks (e.g., 36). Ants of *M. pharaonis* can use the angle of one branch of the trail relative to another to get rapidly back to a larger trunk of the tree or eventually to a nest (21, 74). Second, there are several different trail pheromones: a short-term attractant, a longer-term attractant, and a repellent pheromone. These increase the probability that ants will abandon a depleted source and instead turn around and head back toward the base of the tree, making them available for recruitment to a new food sources (67, 109, 110).

The turtle ant *C. goniodontus* provides an example of a very different system of trail networks. It is an arboreal species with small colonies of up to 1,000 ants, found only in the tropical dry forest, where it is not especially abundant. Its trail networks are made on the network of vegetation made up of tangled branches and vines in the tree canopy (55, 59).

The algorithm that regulates trail networks in *C. goniodontus* prioritizes coherence, keeping the ants together on the trail, rather than rapid marshaling of recruits. The trail networks create a circuit that connects nests, several per colony, with temporary trails to food sources. The circuit changes slowly, on the scale of days and weeks (55). Regulation of the trail is local; it appears that the ants lay trail as they walk along (59) and at every junction in the vegetation, between one branch or stem and another, choose the path that has the most pheromone put down by previous ants. However, occasionally, some ants follow an unmarked path; this allows them to find new resources and repair ruptures. When an ant has left the trail and encounters a junction with no pheromone, it is likely to turn back; this tends to keep ants together on the main circuit of trails.

Initiating a new trail is a slow process that requires enough ants to reinforce many junctions. Once established, the trail is difficult to stop, but the ants are easily deterred by certain other species (55). In response to an accidental break caused by the wind or a passing animal, the trail is quickly repaired and almost impossible to stop. In field experiments in which trails were ruptured, the ants use what is referred to as breadth-first search to go to the next nearest junction and try that one; this contributes to keeping the ants close to the trail. Over time, the trail networks prune away junctions and lose unnecessary loops (59), which further decreases the chances that an ant can wander off the trail and get lost.

The differences in the trail network algorithms of *M. pharaonis* and *C. goniodontus* reflect differences in their ecology (**Figure 1**). The behavior of *M. pharaonis* fits an unstable environment, where competition for food is high and short-term threats are frequent. Its success as an invasive species suggests the capacity to deal with many kinds of environments, to easily find new sources (43), and to respond rapidly to threats and disturbance (124). Large colony size, rapid reproduction, the presence of repletes to buffer food shortages (9), and ability to tune the balance of protein and carbohydrate consumption [for example, to adjust their choice of mint apple jelly or pureed raw ox liver (33)] are all consistent with the hypothesis that the ratio of intake to energy spent is high.

Foraging behavior that strongly emphasizes recruitment rather than individual search suggests that *M. pharaonis* specializes on patchy resources. Recruitment off the trails to create new branches, the use of repellent pheromones, and network structures that funnel ants back toward where they can be recruited again all make the regulation of trail networks based more on local information than on information spatially centralized at the nest. This permits rapid increases in the numbers of ants at food sources.

By contrast, the turtle ant *C. goniodontus* lives in a moderately stable environment in which its movement is constrained by the fixed topology of the vegetation in which the ants travel. Little is known about what this species eats, besides patchy nectar or lichen resources, but they may collect scattered resources as well. Because they have nitrogen-fixing bacteria (71, 113), they may not have to forage for protein.

The algorithm that generates the trail networks of *C. goniodontus* (17, 59) reflects these environmental dynamics. Their networks are regulated to keep the ants on a stable and coherent circuit linking nests and food sources. Foraging rate can be amplified through local recruitment at a particular node. Movement along the main circuit is difficult to stop, even when the trail is ruptured, but foragers on the trail are easily deterred by other species (55). Coherence is prioritized over finding the shortest path, which suggests that movement along the circuit does not have high costs.

CONCLUSION

Figure 1 provides examples of the relation between the algorithms for collective behavior in ants and the dynamics of their environments. Even for the six types of ants described here, there is still much to learn about both their ecology and the processes that generate collective behavior.

It is striking that we know much more about the collective behavior of species adapted to highly unstable than to stable ecological conditions. The species that have been studied most intensively, including *M. pharaonis*, *P. dentata*, and several *Tetramorium* species, respond readily to perturbation, apparently because they have evolved to deal with rapid change. As a result, they are easy to keep in the lab and easily induced to do things people want to study, such as move to new nests and form trails. It would be interesting to learn more about the collective behavior of ant species whose ecology is more stable. For example, little is known about the regulation of collective behavior in the red wood ants of the *Formica rufa* group. They live in very stable

environments, using the same nests and trails to collect honeydew from scale insects in the same trees, and foraging is regulated very slowly from the nest; individual ants show strong trail fidelity, and new trails are difficult to instigate (34, 63). More generally, to learn about the ecological conditions that shape the evolution of collective behavior, we need more studies of the collective behavior of ants in the field.

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