Collect Wis

SOCIAL BEHAVIOR

Ant colonies work without central control. Knowing how they do this might help us understand other systems that have no leader, from brains to the Internet

By Deborah M. Gordon

In the 2015 summer blockbuster *Ant-Man,* the character Hank Pym, a scientist who has invented a suit that can shrink a person down to the size of an insect, remarks that ants can perform amazing feats, but they need a leader to tell them what to do. Pym wears a small device behind his ear that allows him to instruct the ants to act as a phalanx of attackers that helps the ant-sized human hero defeat an evil mastermind.

The idea that ants have commanders that set the agenda and orchestrate their activities resonates because of the hierarchical way in which many human organizations work, and it provides a convenient premise for a Hollywood film whose heroes are people. There's just one problem: it's wrong. Ants never march in lockstep, united in obedience to a single command. In the real world, the often random and apparently inept actions of individual ants, each without any sense of a common goal, combine to allow colonies to find and collect food, build nests, form trails and bridges, defend their host plants from herbivores or cultivate gardens—all without supervision. Ants

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do not need a leader, and no ant ever tells another what to do.

Ant colonies are not the only systems in nature to operate without central control. Collective behavior, without instruction from on high, occurs everywhere, from the flock of starlings that wheels in the sky to the network of neurons that allows you to read this sentence to the molecules that work with genes to make proteins. All the many outcomes of collective behavior are accomplished through simple interactions among the individual actors, whether they are ants, birds, neurons or molecules.

When as a graduate student I began to study systems without central control, I looked for a system in which the interactions were easy to observe—and ants were not hard to find. There are more than 14,000 species distributed across every terrestrial habitat on Earth. They build nests in the ground, in hollow twigs and acorns, under rocks and in leaves high up in the forest canopy. They vary enormously in what they eat, from nectar to fungi to other insects. All ant species exhibit collective behavior, so they provide an excellent opportunity to learn how such behavior has evolved to solve the diverse ecological problems that ant colonies encounter.

My studies of several kinds of ants in a variety of ecological settings, from desert to tropical forest, show that they each use interactions differently—for example, to ramp up activity, slow it down or just keep it going. These findings suggest a fit between the ecological situation and the way that simple interactions adjust collective behavior. Evolution may have converged in a range of systems without central control to produce similar algorithms to meet similar environmental challenges.

Deborah M. Gordon is a biologist at Stanford University. Her research focuses on collective behavior in ants.

SIMPLE INTERACTIONS

ALL ANT SPECIES have certain characteristics in common, including similarities in how the ants carry out tasks. Ants live in colonies composed of many sterile female workers (the ants you see walking around) and one or more fertile females that remain inside the nest. Although these fertile females are called queens, they do not wield any political power—all they do is lay the eggs. Neither the queen nor any other ant can assess what needs to be done and give orders to others. In addition, all ants possess a keen sense of smell capable of distinguishing among hundreds of chemicals. Ants smell with their antennae. When one ant touches another with its antennae, it assesses the odor carried in the other ant's greasy outer coating of so-called cuticular hydrocarbons, which help to prevent desiccation. Scientists know that in some species the chemistry of the cuticular hydrocarbons responds to environmental conditions. A harvester ant that forages out in the hot desert sun comes to smell differently from an ant that spends most of its time in the nest. As a result, an ant's odor reflects its task.

To learn how ants use antennal contacts, Michael Greene of the University of Colorado Denver and I conducted experiments in which we coated small glass beads with extracts of the cuticular hydrocarbons from ants that carry out particular tasks, and then we introduced the beads inside ant nests. We found that when one ant touches another with its antennae, the message it receives is simply that it has met an ant of that particular odor. It turns out the rate of interactions is key to how the insect responds. In our experiments we were able to elicit changes in a colony's behavior by changing the frequency of the ants' encounters with the glass beads.

How do ant colonies organize their work using only simple olfactory interactions? For the past 30 years I have been studying harvester ants in the southwestern U.S. It seems that for harvester ants, the need to conserve water has been a driving force in the evolution of the process that uses interactions to regulate foraging activity. Harvester ants subsist on the seeds of grasses and annual plants, which provide both food and water to the colony. But a colony must spend water to get water. Foragers lose water just by being outside searching for seeds. An outgoing forager does not leave the nest until it has had enough encounters with foragers returning with food. Because each forager searches until it finds food, this feedback from returning foragers links foraging activity to the amount 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.

My long-term study of a population of harvester ant colonies has made it possible to learn how evolution is shaping their collective behavior. To understand how natural selection is currently acting, we needed to know whether the way that a colony regulates its foraging activity influences its ability to produce offspring colonies. The first step was to figure out which colonies were the offspring of which parent colonies. No one had ever made such a determination for ant colonies before. But since 1985 I have been following a population of about 300 colonies at a site in southeastern Arizona. Every year I find all the colonies that were there the year before, say good-bye to the ones that have died and put the newly founded colonies on a map. These long-term data show that a colony lives for 25 to 30 years. Each year there is a mating aggregation that brings together the males, which live only long enough to mate, and unmated queens, from all the colonies in the population. After mating, the males die, and the newly mated queens fly off to start new colonies. Each queen produces a new batch of sterile workers—and, once the colony is large enough, the fertile males and females—every year for the rest of her life, using the sperm she obtains at that original mating session. Based on DNA obtained from about 250 colonies, Krista Ingram of Colgate University, Anna Pilko of the University of California, San Diego, and I were able to link offspring colonies to their parent colonies and thus learn how a colony's foraging activity relates to its reproductive success.

We found that the colonies with offspring colonies tend to be those that conserve water by reducing foraging on hot, dry days, sacrificing food intake to conserve water. This result surprised us because many studies of animals assume that the more food they get, the better. But the colonies that for years I thought were unreliable and wimpy, because they do not forage much when it is hot and dry, turned out to be great-grandmothers, whereas our most stellar colonies, which forage steadily every day, had failed to reproduce. Because colonies can store seeds for a long time, there is no survival cost for not foraging on some days.

Natural selection operates on traits that can be passed from parent to offspring, and there is intriguing evidence for the heritability of collective behavior in harvester ants: offspring colonies resemble parent colonies in which days they choose to reduce foraging. Thus, our findings have provided what is, to my knowledge, the first demonstration of the current evolution of collective behavior in a wild population of animals.

ECOLOGICAL SOLUTIONS

DIFFERENT SPECIES OF ANTS show how the regime of interactions a species uses is related to its ecology. I also study turtle ants that live in the trees in the tropical forest of western Mexico. The air is very humid, and food is plentiful in the tropics, so operating costs of foraging are low there compared with the desert. But competition is high because many other ant species are exploiting the same resources. I found that turtle ant colonies create arboreal foraging trails along which ants perpetually circle from one nest or food source to another. Unlike harvester ants, turtle ant foragers keep going unless interactions lead them to stop or slow down. For example, interactions with ants of other species inhibit activity. A turtle ant is likely to leave the nest and to con-

IN BRIEF

Ant colonies work without a leader. They organize their activities using simple interactions based on scent. **The system of interactions** that a colony uses is related to its ecology. **Insights into collective behavior** in ants could illuminate other systems that operate without central control.

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tinue on the trail unless it meets an ant of another species. Just one *Pseudomyrmex* ant strutting back and forth on a branch, sleek and severe like a sports car, can meet enough of the stockier yet more timid turtle ants to completely shut down a branch of their trail. Colonies are so persistent in maintaining the flow of ants on a trail when all is clear, and starting it again once a threat disappears, that perhaps it is easiest to avoid conflict.

Simple interactions among ants create the turtle ant colony's network of trails within the tangled vegetation of the forest canopy. Those interactions make the network both resilient and flexible. Every ant marks its route with a chemical trail pheromone as it goes and follows the scent of the ants that came before it. Saket Navlakha of the Salk Institute for Biological Studies and I are working to understand the algorithm that the ants use to maintain and repair their trails. When an ant reaches a junction between one twig, stem or vine and another, it tends to take the path that smells the strongest of trail pheromone, which is the path most recently traveled by the most ants. Often a tenuous bridge between one stem and another falls away because of the wind, a passing lizard, a break in a rotting branch or, sometimes, an experimental intervention from my scissors. The ants recover quickly. It seems that when they reach the first broken edge, the ants go back to the next available node and search for the pheromone trail from there until they form and eventually prune a new path to join the other side of the path.

Collective behavior in ants has evolved in response to how resources such as food are distributed in the environment, as well as to the costs of foraging and the behavior of other species that they meet. Some resources are clustered together in a single patch, whereas others are scattered at random. Ants of many species excel at exploiting patchy resources such as picnics. They use interactions based on pheromones in which one ant follows another, producing recruitment trails. Recruitment makes sense when the resource is patchy—after all, where there are sandwiches, there are likely to be cookies. In contrast, ants that forage for scattered resources, like seeds, do not use recruitment trails, because finding one seed is no guarantee of finding another nearby.

To find food in the first place also requires specialized collective behavior. Because ants operate mostly by smell, an ant must get close to food to find it. The broader the range of places where food might be, the more area the ants must cover. But the more different places it could be tucked away, the more thoroughly searchers must scour the ground. I found that Argentine ants manage this trade-off beautifully, by adjusting their paths according to density. When there are few ants in a small space, each ant takes a convoluted path, allowing it to search the local area very thoroughly. But when there are few ants in a large space, they use straighter paths, which allows the entire group to cover more ground. Individuals could sense density by a simple cue: the rate of interactions with others. The more antennal contacts they make, the more convoluted a route they take. The Argentine ant has invaded Mediterranean climates throughout the world. Perhaps its effectiveness at getting to new food resources first explains why this invasive species tends to outcompete native species wherever it invades.

LESSONS FROM ANTS

THE WAYS ANTS USE simple interactions to thrive in particular environments could suggest solutions to problems that arise in other systems. Computer scientist Balaji Prabhakar of Stanford University and I noticed that the harvester ants use an algorithm to regulate foraging that is similar to the transition-control protocol/Internet protocol (TCP/IP) used in the Internet to regulate data traffic. We called the analogy the "Anternet." TCP-IP was designed in an environment with high operating costs: the early Internet was so small that there was little redundancy, and ensuring that no data packet would be lost was crucial. Just as a forager will not leave on its next trip unless it has a sufficient number of interactions with returning foragers that have found food, so a data packet will not leave the source computer unless it receives an acknowledgment from the router that the previous packet had the bandwidth to travel on toward its destination. It seems likely that 130 million years of ant evolution have produced many other useful algorithms that humans have not yet thought of and that could help us figure out ways to organize data networks using simple interactions involving minimal information.

I think that we will probably see a similar fit between algorithm and ecological situation in many other kinds of collective behavior. For example, cancers evolve in response to the conditions in their local microenvironment. A type of cancer that tends to metastasize to a particular kind of tissue probably evolves to use resources clustered in that tissue. These forms of cancer, like the species of ants that have evolved to use patchy resources, may be the most likely to send cells back to the primary tumor to recruit more cells, as breast cancer cells do. In that case, cells that recruit to patchy resources would be the best target for poison baits.

Throughout biology and engineering there is an explosion of interest in how collective behavior draws on simple interactions. It is becoming clear that such interactions are tuned to changing conditions. The field of systems biology, building on a century of work that showed in detail what happens inside a cell, is shifting its focus to interactions among cells, aided by amazing advances in imaging. In neuroscience, new techniques allow recordings that show patterns in the timing of thousands of neurons firing. We humans can see certain kinds of movement and hear certain sounds because circuits of neurons in our brains have evolved to respond collectively to features of the environment such as the rate at which crucial objects, such as parents and predators, usually move, and to the range of frequencies that it was most important to be able to hear. Engineered systems evolve as well; enormous increases in the size of the Internet and the number of devices connected to it, as well as the speed of interactions, require new, decentralized solutions.

Scientists are now ready to look for trends in the ways that different natural systems have evolved similar collective behavior to meet similar ecological challenges. We may be able to apply that knowledge to intervene in processes that work without central control—and solve some of society's problems in the process. SA

MORE TO EXPLORE

Ant Encounters. Deborah M. Gordon. Princeton University Press, 2010.

The Ecology of Collective Behavior. Deborah M. Gordon in *PLOS Biology,* Vol. 12, No. 3, Article No. e1001805; March 11, 2014.

FROM OUR ARCHIVES

Swarm Smarts. Eric Bonabeau and Guy Théraulaz; March 2000.

scientificamerican.com/magazine/sa