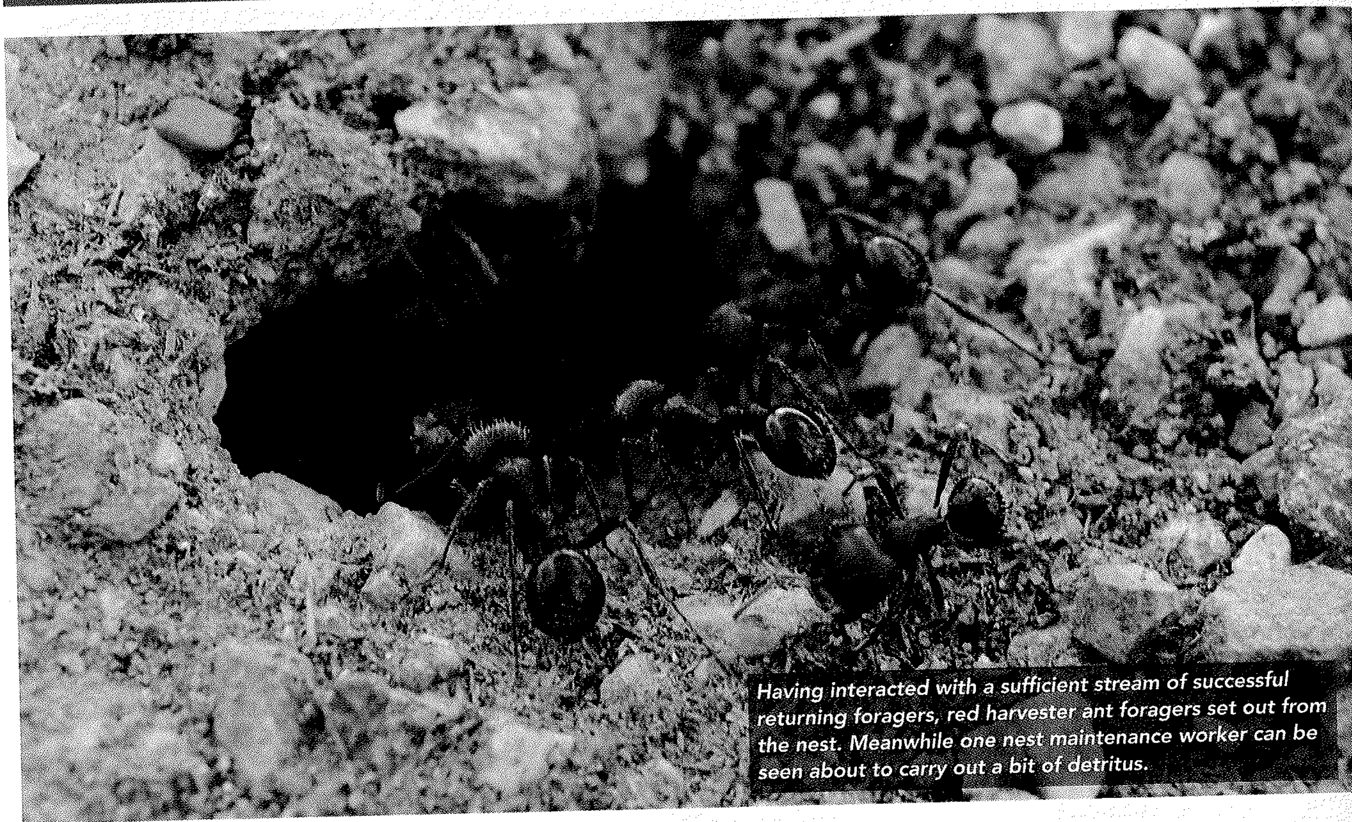

Having interacted with a sufficient stream of successful returning foragers, red harvester ant foragers set out from the nest. Meanwhile one nest maintenance worker can be seen about to carry out a bit of detritus.

KATIE DEKTAR

Twitter in the Ant Nest

How does a colony organize its work?

By Deborah M. Gordon

Ant colonies work without central control. If you've seen any of the recent movies set in an ant colony—*Antz, It's a Bug's Life, The Ant Bully*—you saw generals, bureaucrats, and foremen bossing around whoever is on the next rung down the social ladder. None of those managers exist. No ant gives instructions to another ant, or decides for another what needs to be done.

Yet ants as a group are astonishingly successful. After more than 100 million years of diversifying into every habitat on the land surface of the Earth, there are now more than 12,000 known species of ants. Very few have been studied in detail, but we know that all live in colonies, with one or more reproductive females that lay the eggs while other females, the workers—sterile in most species—do everything else. It takes a whole colony to produce the daughter queens that found new colonies. A colony, not an ant, is the reproductive individual.

Ant colonies accomplish many tasks. In all species, the ants make or find nests, collect food, care for their young, and get rid of waste. There is infinite variety on that basic plan, from species that move their whole colonies frequently to those that build nests that last for decades; from species that kill live prey to those that tend fungi to eat; from species that raise huge colonies to those that steal workers from another species.

If you watch ants for a while, you will probably be impressed by their ineptitude. Yet all the failed attempts—pairs of ants pulling objects in opposite directions, ants taking the longest possible way to get from point A to point B—still add up to success: enough ants get it right enough of the time that things get done.

Without anyone in charge, colonies respond effectively to a changing world. Stuff happens to an ant colony, as it does to any organism, and the colony reacts by adjusting the ef-

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A red harvester ant forager sets out to search for a seed. In this species, each forager searches independently, rather than following a trail laid down by nestmates.

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fort devoted to each task. When the nest is crushed by a passing mammal, how does the colony decide which, and how many, ants will repair it? Colonies have to react to good times as well as to bad. Everyone knows that where there is a picnic, there will be ants. How does the colony decide how many ants to send to the picnic, and which ones?

I call the process that adjusts colony effort to the current situation "task allocation." Although no one assigns an ant a task, the colony manages to organize itself as needed. Task allocation depends on local interactions among ants, none of which can make a global assessment about what needs to be done. In fact, most ants can't see very well and operate largely by smell. To interact, ants must get close to each other.

Along with collaborators and students in my lab team at Stanford University, I have been studying task allocation as part of a long-term study of the behavior and ecology of the red harvester ant, *Pogonomyrmex barbatus*. We observe a population of about 300 colonies in the desert grassland and chaparral in the southeastern corner of Arizona. Because I census the population each year, I know each colony's age and have learned that colonies live for about twenty-five years. A colony is founded by a single queen, which produces all the ants in the colony over her twenty-five-year lifetime, using sperm from an original mating session. After the queen dies, once all of the workers have died, the colony dies too.

Harvester ant colonies perform four tasks outside the nest. *Patrollers* are the first ants to leave the nest in the morning. They meander around the nest mound and foraging area, then return. It is their return that initiates foraging. *Foragers* leave the nest in streams, fan out to search for seeds, then bring the seeds back to the nest. Those ants do not collect food that takes more than one ant to carry, and so do not use pheromone trails to recruit other ants. Instead, each ant searches individually for a seed, which could be scattered anywhere or buried in the soil.

Meanwhile, two other task groups stay close to the nest. *Nest maintenance workers* mostly work inside the nest, constructing new chambers and tunnels, and lining the walls of the existing chambers with moist soil that dries to a smooth adobe surface. They also come out of the nest in groups, each carrying a particle of dry sand or seed husk; go out to the day's dumping ground on the nest mound, maybe five or ten inches from the nest entrance; and then turn around and go right back into the nest. Finally, *midden workers* toil over the refuse pile and over the pebbles that the ants bring back to cover the mound. We have just learned that those pebbles carry a colony-specific odor, and Shelby Sturgis, a graduate student in my lab, is investigating whether and how often the midden workers renew the odor on the pebbles.

Ants switch tasks. I learned this by marking ants with colored paint. Once the paint dries, a marked ant recovers its usual smell, and because their vision is so poor, the other ants are unaware of the spectacular fashion statement it is making. Although individuals switch tasks, not all transitions are possible. When more ants are needed to forage, ants at work in any other capacity—patrollers, midden workers, or nest maintenance workers—may drop that task and take up foraging. When more patrollers are needed owing to some disturbance, nest maintenance workers may become patrollers. But when more nest maintenance workers are needed, they must be recruited from among the younger ants inside the nest. Once an ant has left nest maintenance work to become a patroller, midden worker, or forager, it will not go back to nest maintenance. There is a flow from the younger ants inside the nest toward outside tasks, ending in foraging. Because colonies are competing with one another for food, it makes sense that the task-switching system channels more ants into foraging when more food becomes available.

An ant makes moment-to-moment decisions about which task to perform, and also whether to perform it actively at that moment. No one is directing ants in their decisions, and each ant must use immediate, nearby cues. Some of the cues are in the ant's environment. If ants did not react to the discovery of food, no ants would show up at a picnic. Other cues are from other ants. An ant's behavior also depends on its recent rate of interaction with other ants.

Ever see ants touch antennae? That simple interaction is the pulse of the colony. Ants smell with their antennae. When one ant contacts another, it can smell whether the other one is a nestmate. Like all Hymenoptera—ants, bees, and wasps—ants are covered with a greasy layer of hydrocarbons that helps keep the insect from drying out. The cuticular hydrocarbons, secreted from a gland in the ant's mouthparts and spread around by grooming, carry a colony-specific odor. We found that in harvester ants, as in the few other species that have been studied this closely, the hydrocarbon profile identifies an ant's task as well as its colony. In the mid-1990s, Diane Wagner (now an associate professor of biology at University of Alaska Fairbanks) and others in my lab found that the conditions in which an ant works modify its odor. The longer an ant spends outside in the hot, dry air of the desert, the higher the proportion of so-called *n*-alkanes in its hydrocarbon profile.

When an ant contacts another with its antennae, it uses the cuticular hydrocarbon profile of the other ant to assess its task. Michael J. Greene (now an associate professor of biology at the University of Colorado at Denver) and I showed this in field experiments using small glass beads (about two millimeters in diameter) as stand-ins for ants. My earlier work had shown that the return of the patrollers initiates foraging: if the returning patrollers were collected and kept in a plastic box so they couldn't go back in the nest, the foragers did not come out. This time we intercepted the patrollers, and in their stead dropped into the nest glass beads coated with an extract of patroller cuticular hydrocarbons. We compared how much colonies foraged in response to the return of live patrollers, beads with patroller hydrocarbon extract, beads with just the solvent, and beads with nest maintenance worker hydrocarbons. Beads with the odor of patrollers brought out the foragers while the other beads did not.

Foragers need to meet something that smells like a patroller in order to start foraging, and an inert glass bead does just fine. There is no message in the interaction. The patroller doesn't tell the forager to go out; the odor just tells the forager that it met a patroller that returned. If a patroller can get out and back in again without getting blown away by the wind or eaten by a predatory horned lizard, then it's safe for a forager to go out.

The rate of interaction is important. We dropped beads into the nest at different rates, and foraging was stimulated best by beads introduced at the rate of one every ten seconds—the rate that patrollers typically come in when the coast is clear and that normally stimulates foraging. It seems that an interaction stimulates a response, but its effect decays after ten seconds or so. If the ant is stimulated often enough, it leaves the nest. If encounters happen too infrequently, the ant forgets all about it between encounters, and just stays inside. Whether a forager goes out for the first time each day depends merely on how often it meets something that smells like a patroller.

Once foraging begins, the rate of interaction with returning, successful foragers determines the intensity of foraging. Each forager leaves the nest, travels out with a stream of foragers for a while, then stops to search the ground carefully for a seed. Once it finds a seed, it comes immediately back to the nest. How long it spends outside the nest depends mostly on how long it has to search. Thus, on a day when there is abundant food, foragers find it easily and return quickly. When a forager returns from its trip, it drops its seed in the chamber inside the nest for other ants working inside the nest to deal with, and becomes an inactive forager, waiting to go out again. How soon it goes out is set by the rate at which food-bearing foragers come back in. When we remove foragers returning to the nest with seeds, the rate at which foragers go out quickly drops. When we remove returning unsuccessful foragers, it makes no difference to the rate of forager outflow.

Although no ant knows how much food there is, this system allows the colony to tune its foraging very rapidly to the availability of food. The rate of forager return reflects food availability. No ant tells another anything at all, but the colony uses interactions between outbound foragers waiting inside the nest, and successful foragers coming back into the nest, to measure the benefits of sending out more ants.

The interactions of incoming and outgoing foragers regulate foraging according to current conditions, but (unlike pheromone trails) do not convey any specific information about the location of food. Each individual ant usually goes to and returns from one site over and over during a given day, wherever it was successful on its first trip of the day; its return stimulates other foragers to set out, but each goes in its own direction. Food availability is set by widespread conditions such as whether the wind has blown in many seeds, or recent rain has uncovered seeds in the upper layer of the soil. If food is abundant for the ants in one direction, it is probably a good time to forage in another direction, too.

We have learned that colonies differ in how closely they regulate foraging. In addition to the availability food, an important condition that affects forgaging success is water stress. Out in the hot sun, these ants use water, which they obtain from the seeds by metabolizing the fats. Perhaps colonies that make better decisions about how many ants to send out, given the day's humidity and the amount of food available, improve their own survival and reproductive success. Some colonies are more sensitive than others to changes in the rate of forager return. We are now working to learn whether those colonies that thereby fine-tune their foraging are producing more offspring than the more stoic colonies that plod along without changing foraging activity very much.

It is becoming clear that interaction networks drive the behavior of social insect colonies in many ways. For example, ants encounter workers both from their own colony and from other colonies. The rate of those interactions enables the workers to compare the relative numbers of "Us" versus "Them"; ants may react more aggressively when heavily outnumbered. In acorn ants, colonies use the rate of interaction to decide which of the options for a new nest site has become more populated with satisfied scouts.

Argentine ants appear to use interaction networks to adjust their searching to local nestmate density. The shape of an ant's path depends on how many other ants are nearby: it searches more intensively in its immediate vicinity when there are more ants close by, but stretches out its path to cover more ground when there are fewer ants around to help search. Fire ants speed up their interaction rate around food; perhaps this helps to speed up recruitment. Pheromone trails are another example of an interaction network. An ant responds to a chemical left behind by one that passed by a few moments ago, which simply says "an ant was here," and in the aggregate, many ants end up at the food source.

Ant colonies have perfected a system that regulates the behavior of large numbers of ignorant participants. Their individual responses are guided by interactions that convey little information except the fact that two ants met. A social insect colony is ticking with these brief interactions, and uses this pulse to adjust its response to the world.

In some ways, human society is becoming increasingly ant-like. The rate of Internet interactions sets the rhythm of our purchases, our work, and our social connections. We use interaction networks in engineering; for example, distributed algorithms allow a group of robots to map a fire scene, attack an enemy, or photograph the surface of another planet. But unlike the ants' networks, ours are shaped by our motives, feelings, and identity. Watching ants, we have to wonder how much difference that makes.

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