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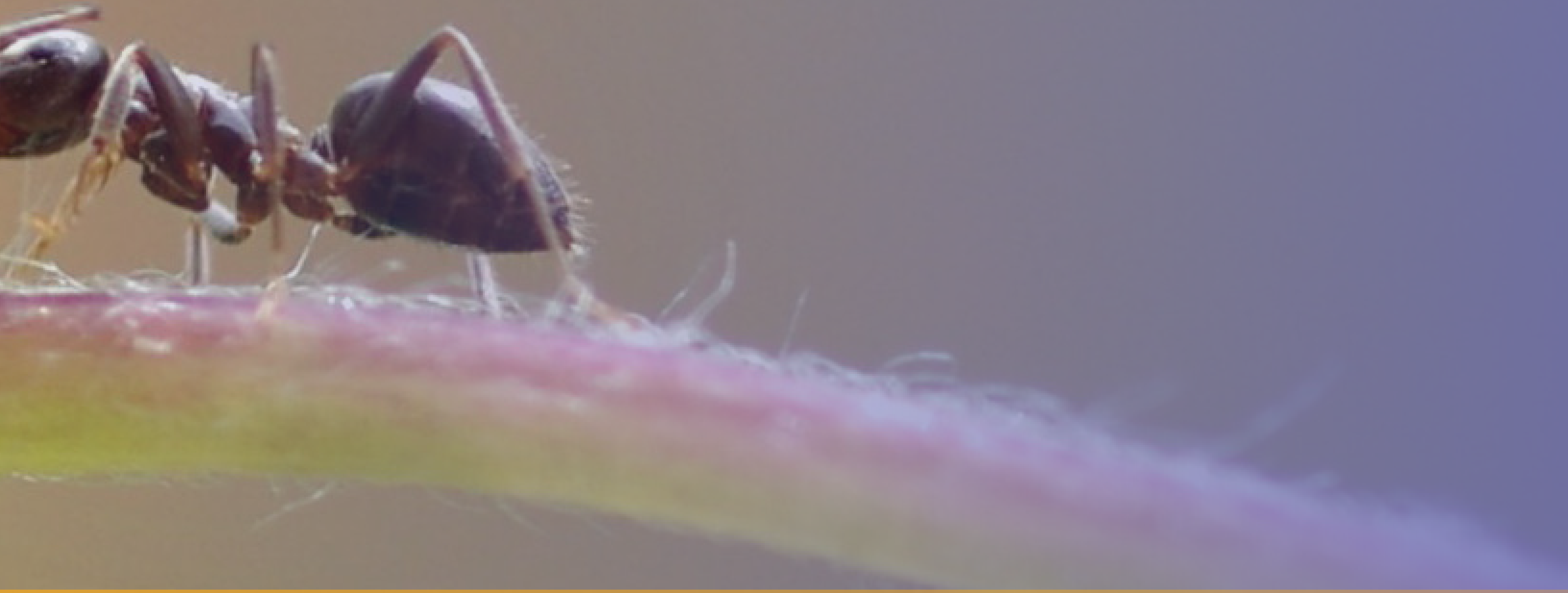
All for One and One for All

The Emergent Intelligence of Ant Colonies



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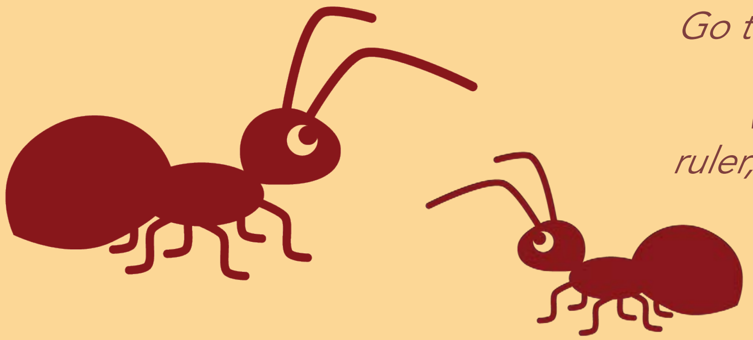
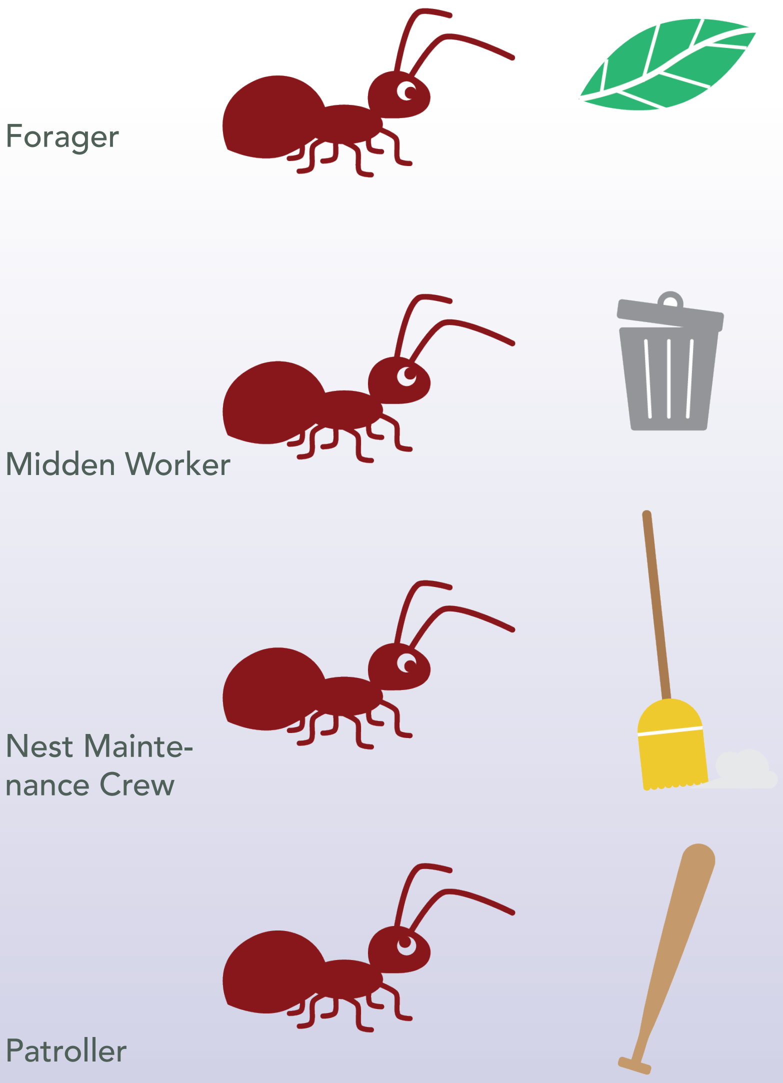


Go to the ant, O sluggard; consider her
ways, and be wise.
Without having any chief, officer, or
ruler, she prepares her bread in summer
and gathers her food in harvest.
(Proverbs 6:6-8)

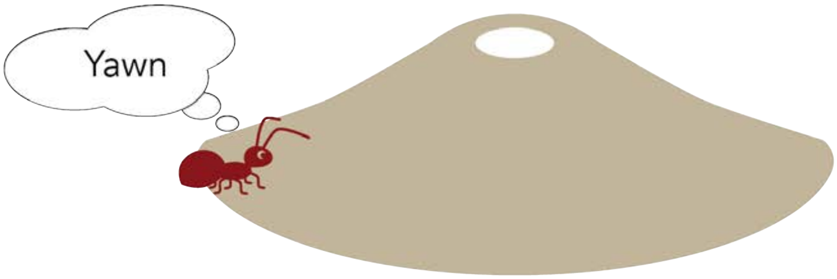
For the past thirty years, Deborah Gordon has returned to the same patch of desert in northeast Arizona to visit old friends. They are the most loyal companions, always emerging from their clay-lined huts in the earth to greet her (and the annual treats that she brings). To Gordon, the desert represents a community far removed from her home in Silicon Valley. She celebrates the birth of new members and the death of old matriarchs. She rejoices with old friends when they become mothers, grandmothers, and great-grandmothers, doting over the resemblances she observes. She takes note of those who perish to floods, droughts and famine, as well as those who survive. She is mindful of rivalries. It is a bustling village—a bustling *oikos*, to use the Greek translation of the word. There is perhaps no one better than Gordon to explain why *oikos* is the etymology of modern day *ecology*.

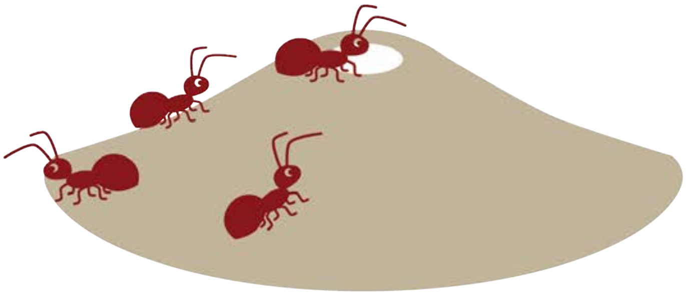
Deborah Gordon is a Professor of Biology at Stanford University, so perhaps you are unsurprised that her old friends are not human. You might, however, be surprised to learn that they are not individual ants, either. Gordon goes back to the desert every year to check up on. A single ant lives only for about two years, but a colony may live well into its early-30s. And, like all reproducing organisms, colonies have the potential to live on through their offspring. “Ants never make more ants; colonies make more colonies,” Gordon explained in her acclaimed 2003 TED talk. Every year, on the same day, winged reproductive ants emerge from their colony and carry out a mating flight, during which a single female mates with many males before landing in the sand and burrowing into the ground. She then begins laying her eggs, and she will lay eggs from that very mating event for the next 15 to 20 years, never again emerging from the earth. She has become a queen, and a new colony carrying



the same genetic material—a daughter colony, so to speak—has been born.

Gordon is not the first scientist to consider the possibility that the colony itself functions as a unified organism. Throughout the history of biological study, there have been many definitions proposed of what it means to be an "organism." In 1852, Aldous Huxley defined an organism as "the sum of the phenomena presented by a single life."[1] This definition was amended over time to include notions such as the assimilation of substances, reproduction of similar systems and subjection to the laws of natural selection.[2,3] Perhaps the most prevailing definition today, however, is that an "organism" is any combination of parts that acts in nearly complete cooperation and has no affiliations outside the self.[4] By this definition, in particular, the ant colony certainly qualifies.





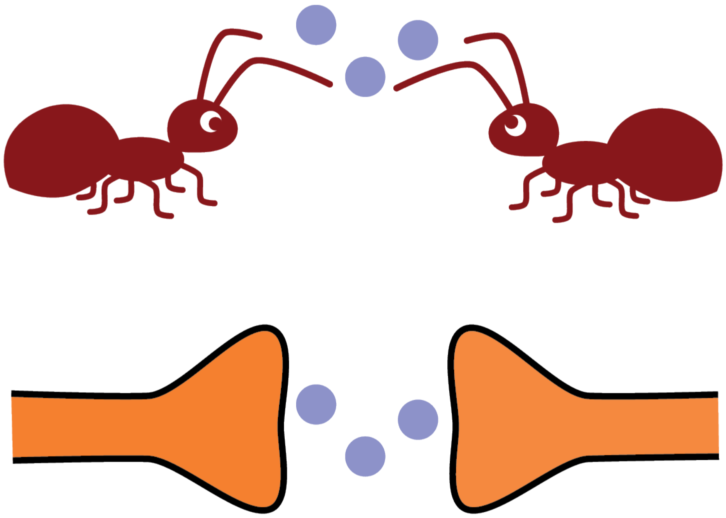
You may be thinking: What of the individual ant? Surely an ant is an organism. And while this is true by most all definitions, studying an ant in the context of its colony requires a shift in perspective. Individual ants are rather simple. They are designed to integrate local signals in order to make binary decisions—to act or not to act. Some ants patrol the nest perimeters, others forage for food. Some ants maintain the cleanliness of the nest, others take out the waste. Still others lie dormant in the earth, providing a living shield to protect the queen and her precious eggs. But all ants are dependent on other ants. In a community, they can survive. In isolation, they will most certainly die.[5]

Although ants are simple-minded, the colony itself is exhibits remarkably complex behaviors. Take, for example, the way in which ant colonies respond promptly and collaboratively to the appearance of food, and in numbers that precisely reflect the amount of food present. How does a colony know how to "behave," and how is this behavior so flexible? It might seem reasonable to believe that the queen is in control, perhaps by sending out specialized chemical cues to various parts of the nest in order to govern the ants in any given vicinity. This, however, is not the case. Even if the queen were able to send out specialized chemical signals to specific groups of ants, it would be impossible for her to have enough information of the outside world (or of the nest conditions itself) to offer effective instructions to the other thousands of ants in the colony. Importantly, an ant colony is able to respond to environmental conditions without centralized control. It is an organization made of up thousands of parts all operating collaboratively within a complex network of interactions. The dynamic communication between ants in a colony allows for the emergence of collective, intelligent behavior; and in this way, ant colonies are exquisitely similar to animal brains.[6]

In order to understand what I mean, let us start by considering how a Red Harvester colony in the Arizona desert employs forager ants to find seeds. The underlying principle is simple: a forager ant will leave the nest in search of seeds and it will not come back to the nest until it finds one. If there are many seeds in the nest vicinity, then the forager ant will return quickly. Its prompt return to the nest will signal to other forager ants that there is food within close proximity, triggering their own deployment. Thus, the rate at which forager ants return to the nest determines the rate at which forager ants leave the nest. In this way, the colony does not waste individuals when there is no real promise of food in its environment.[7,8]

When this model of ant colony foraging surfaced in biological journals, it caught the attention of one prominent neuroscientist working just south of Deborah Gordon. Michael Goldman is a neuroscientist from UC Davis who has spent much of his career working to understand the decision-making properties of neurons. Before reading Gordon's study, Goldman had worked using computational modeling to understand the relationship between neuron properties and network function. Specifically, Gordon was interested in how the willingness of individual neurons to fire affected the behavior of circuits.[9] When he read Gordon's work, he was inspired by the collective behavior of the ants as well as their striking similarity to neurons in a brain. He reasoned that it was perhaps possible to use ants to study the brain—and the brain to study ants.

Imagine for a moment, that a colony is a brain and that each neuron is a forager ant at the nest. A returning forager ant is the equivalent of an incoming action potential; when it makes contact with a sedentary ant back at the nest, it "excites" it, triggering a new departure—a new "action potential," so to speak, that will eventually come back and reach another "neuron." The more food there is, the more forager ants will return to the nest to excite new waves of foragers. This positive feedback will continue until the food source dwindles, the rate of returning ants slows, and the activation of new forager ants falls back to a "resting state." Importantly, just as a forager ant might be "excited" to pursue food in its environment, it might also be "inhibited" to retreat back to the safety of the deep nest if a lack of returning ants signals that there is no food around to respond to. This operating system parallels the way in which neurons respond to environmental stimulus; through simple networks of excitation and inhibition.



Gordon and Goldman applied mathematical models to understand the dynamics of ant foraging feedback.[10] Intuitively, Gordon and Goldman found that ants that left the nest to forage had experienced a higher rate of interaction with returning forager ants than those that returned to the depths of the nest. They also found that forager ants at the nest accumulate experience with returning ants, weighing experiential evidence in order to "decide" whether or not to leave or retreat—synonymous with the "decision" of a neuron to fire or not to fire. To reflect the decision-making process of the individual ants, Gordon and Goldman developed a stochastic accumulation of evidence model to predict the rate of incoming, outgoing ants and retreating ants. Stochastic accumulation of evidence models are used quite often in neuroscience and psychology to understand how noisy environmental information is processed when deciding between two competing choices.[10] From the perspective of a neuron, "noisy environmental evidence" refers to the rate of input it receives from the hundreds or thousands of others neurons to which it might be associated, and the two decisions are to fire or not to fire. From the perspective of the ant, "noisy environmental evidence" refers to the rate at which it encounters returning forager ants, and the two decisions are to leave or to retreat.

How, though, are ants able to identify foragers that are returning versus those that are simply wandering around the nest? When observing an ant colony, the dynamic character of ants is readily apparent; what is less apparent, however, is their tendency to make direct, physical contact with the antennae of other ants in their vicinity. This finding led researchers to investigate the mode of communication employed between members of a colony during brief periods of antennal contact.[11] Scientists discovered that ant communication was first and foremost, chemical, but more specifically, dependent on unique cuticular hydrocarbon profiles present on each ant's antennae. Literature has found cuticular hydrocarbons to be critical for maintaining the social coherence of colonies.[12,13] In the context of Red Harvester forager ants, cuticular hydrocarbon profiles are even different between those who have left the nest and those who have remained. Though the difference is subtle, it is significant enough to be detected by arrays of sensitive receptors on the surface of an ants' antennae such that returners may be identified.[8]

Cuticular hydrocarbons present on each ant's antennae allow us to complete our understanding of Gordon and Goldman's colony-brain model: each colony is a brain, each ant is a neuron, and each cuticular hydrocarbon is a neurotransmitter that serves as chemical communication. Neurons operate in complex networks of branching dendrites and traversing axons; ants operate in complex networks of random movement and stochastic interactions. Both, however, exhibit emergent intelligence as the sum of positive and negative local interactions.[6]

Let us return now to the idea of the colony as an organism—an organism composed of collaborate parts that functions much like a brain. Throughout her time in the desert, Deborah Gordon has worked to understand how environmental pressures lead to the evolution of ant colony behavior. In order to be subject to evolution, a particular trait—be it behavioral or physica—must be subject to natural selection. Natural selection was originally coined by Charles Darwin in the late 19th century and defined as "the principle by which each slight variation in a trait, if useful, is preserved."[14] In other words, a particular trait, if beneficial to the organism, will be passed on to offspring, and over generations it will become increasingly prominent in the population as a whole. Importantly, not only must differences in a trait allow for differential survival and reproductive success, but these differences must also be heritable. That is, they must be encoded in genes so that offspring may experience the same fitness benefits.

We see behavioral evolution in nature all the time: crickets tune their song in response to sexual selection; birds adjust their migratory patterns in response to climate change; squirrels modify their caching behavior in response to resource availability.[15] Although evolution can be observed by comparing traits at the organismal level, the mechanism of evolution is the propagation of certain genes in a population over time. This is perhaps easy to understand in an animal system, but it is complicated when thinking about the evolution of "super-organisms." Can ant colonies evolve in the same way as a squirrel? Is there anything about colony behavior that is, in fact, heritable?

This is a question that Deborah Gordon and her research team set out to answer in the fall of 2010. First, remind yourself that ants never make more ants; colonies make more colonies. In order to understand the family tree of the community she had been studying for decades, Gordon took genetic samples from each of the many hundreds of colonies living within her 250 by 400-meter research site. She was then able to determine which colonies came from which—in other words, which queens were mothers and which were daughters. The ultimate goal was to uncover resemblances between related colonies.

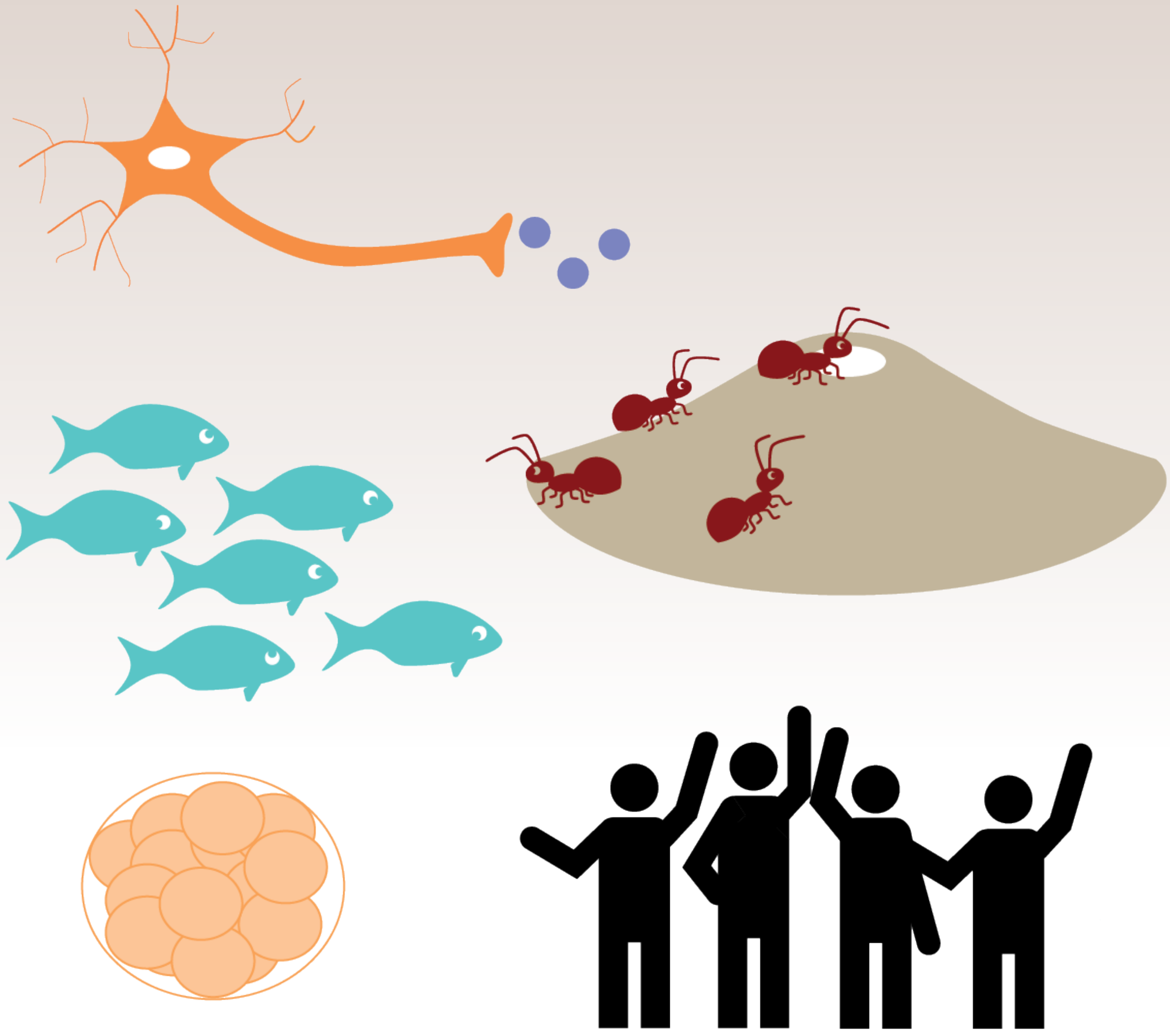
The results were fascinating. She found that one of her favorite colonies—colony 154—had recently become a great-grandmother, and that its daughters, granddaughters and great-granddaughters contributed more significantly to the community structure than any other lineage.[16] It seemed to Gordon that there must be something about colony 154 that made it particularly successful at surviving and reproducing, and that whatever this trait was must be in some way passed on to offspring.

But what, in fact, was this trait? What made colony 154 so much more successful than other lineages competing for the same resources?

The answer was rather counter-intuitive. Colony 154, more than any other colony, was particularly lazy.[17] While other colonies were out and about in the heat of the day searching for food, colony 154 was resting. Its nest-bound foragers were slow to move and required a much higher rate of antennal contacts with returners to rally a search for food. The foragers of colony 154 seemed less inclined to waste away in the hot sun on a hot day than their competitors, and this, it seemed, was serving to their advantage. So, Gordon was compelled to ask: Could "laziness" be a heritable colony behavior?

She found that, indeed, it was. When it came to the willingness to forage, the offspring of colony 154 exhibited undeniable resemblance to their mothers; and when Gordon looked further, she found that these resemblances were rooted in the number of interactions forager ants at the nest must have with returning foragers before they were willing to set out themselves. In other words, the decay rate of antennal interactions was faster in foragers ants of colony 154, requiring that they experience a higher rate of "excitatory" antennal interactions before deciding to leave. Gordon further found that the required rate of antennal contacts was not only consistent between colony 154 and her offspring, but also between the mothers and daughters of other lineages as well. She concluded, therefore, that there must be a genetic component to forager ant response, and that this genetic component offers variation in foraging behavior that produces differential fitness among colonies in a community.[17,18]

If we return again to idea that we can use ants to understand the brain, and the brain to understand ants, we might discover a whole new perspective on what it means to ask questions about collective behavior. Ants may be considered neurons in a brain, but they might also be considered cells in an embryo, fish in a school, or even humans in a mob. Taken individually, a single part means nothing, but taken together, we see patterns of remarkable emergent behavior that may be acted upon by natural selection. Ants show us how understanding the properties of parts sheds light on the function of the whole. And this might just make the thirty years Deborah Gordon spent in the desert entirely worth her time.



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