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12 The Development of Ant Colony Behavior

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Developmental systems theory seeks alternatives to the idea that an organism's development is the expression of information already in place before development began. It is obvious that such alternatives are needed to understand the development of an ant colony. A colony's behavior arises from the relations of ants to each other and to the rest of their environment (Gordon 1999). The colony's behavior can not be the product of prepackaged instructions, because there is nowhere to locate the package. As the colony grows older, the ants die, to be replaced by their younger sisters. The queen lays the eggs but does not direct the behavior of the ants. Each ant's behavior is based on local information. The aggregate of all ants' behavior produces the development of the colony.

An ant colony consists of many sterile female workers and one or more reproductive females or queens. The queen produces new workers. Ant colonies produce offspring colonies, so a colony can be considered as an individual organism: A colony is born, grows older, reproduces and, when the queen dies and there is no one to produce more workers, the colony dies. The behavior of the colony develops, year after year, as new ants are born into the colony and die. This chapter is about the development of colony behavior in the red harvester ant (*Pogonomyrmex barbatus*), a desert species that eats the seeds, mostly of grasses, that it collects from the ground. In a mature harvester ant colony, each summer the queen produces reproductives, winged queens and males who fly off to mate with the reproductives of other colonies. After mating, the males die and the newly mated queens found new colonies. A colony may live for fifteen to twenty years (Gordon 1991), beginning with a single queen and reaching a stable size of about ten thousand workers when the queen, and the colony, are five years old. Individual ants live only a year.

I study a population of about three hundred harvester ant colonies in the desert of southeastern Arizona. Each year I census all of the colonies, which are individually labeled. This census, now in its fifteenth year, tells me how old each colony is, and that has made it possible to track the development of colony behavior, as well as the demography of the population.

A colony's behavior changes as it grows older and larger. Colonies of any age must perform certain tasks, such as building a nest, taking care of the juvenile stages (eggs, larvae, and pupae), and collecting food. Task allocation is the process that adjusts the numbers of workers engaged in each task, in response to changes in the environment and the needs of the colony (Gordon 1996). Task allocation operates differently in young, small colonies and old, large ones. Old colonies respond in a more stable way to environmental perturbations than do younger ones. In addition, young and old colonies differ in their relations with neighboring colonies of the same species.

Ant colony behavior develops as a result of the ants' responses to the changing contexts they experience as the colony grows older. The most obvious change over time in the colony is its size (figure 12.1; Gordon 1992). Colony size thus seems to be the first place to look for explanations for age-dependent changes in colony behavior. In a large colony with many ants, each ant experiences a different environment from the one that surrounded an ant in the smaller, younger colony. Colony size affects the pattern of an ant's interactions with other ants: more ants can lead to a higher rate of contact among ants. Ants modify their environment by creating and modifying a nest, adjusting the amounts of vegetation, refuse and chemical traces on the surface of the nest mound, and by altering through food collection the distribution of food in the foraging area around the nest. More ants modify their environment more, and in different ways.

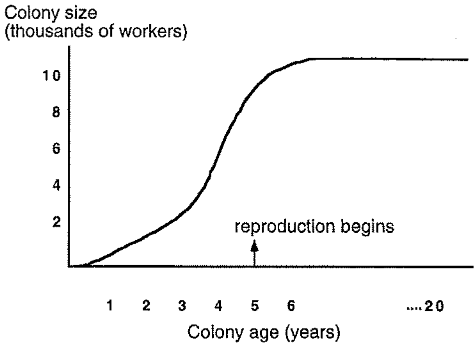

Figure 12.1
How colony size, in numbers of workers, depends on colony age.

A population of colonies thus provides an example of niche construction (*sensu* Lewontin 1983). In harvester ants, this process of niche construction unfolds over the fifteen- to twenty-year lifespan of the colony. To find proximate explanations for the ways colony behavior changes as the colony grows older, we must examine how the colony modifies its environment as it grows larger.

Founding a Colony

The beginning of a colony's development is the stage I know least about. Six to eight weeks after the mating flight, the first workers emerge. These ants are tiny; the queen fed them as larvae from her own fat reserves and they are much smaller than later cohorts of workers. These first ants go out to forage, with only four to six weeks of foraging time remaining before the colony's first winter sends them back inside the nest. By the next summer, the colony will have a small nest with many tunnels and chambers, a small mound above the ground, and five hundred to a thousand ants, and the foragers will begin to explore the neighborhood.

An ant in the first batch of workers emerges from its pupal case into a single tunnel and the company of a few other workers, perhaps some eggs and larvae. Somehow some ants get out and collect some food, and this food is given to the larvae. Some ants must begin to dig. A year later, by the time the colony has reached its first summer, an ant emerging from its pupal case finds a very different environment. An ant in the one-year-old colony is part of a functioning colony. Several tasks are carried out simultaneously. The processes that shuttle ants from one task to another are in place. There is a nest with a system of tunnels and chambers. In a one-year-old colony, ants come barging out of the nest entrance apparently intent on some activity, perhaps heading straight for a foraging trail or ambling over to the midden pile to move bits of refuse from one place to another. But ants in the first batch of workers seem more uncertain (though I have been able to observe them only in the laboratory).

It might be tempting to believe the first forager to walk out of the nest is "programmed" to collect food, bring it back to the nest and feed it to the queen who then produces more and more of these "hard-wired" automata. But there is no reason to believe the first ant to come out has some prior knowledge of what to do, any more than the rest of the ants do. The ant is born in a chamber at the bottom of a straight tunnel. It can go only around the chamber or up the tunnel. Eventually it goes up. It gets outside. Being an ant, the events it encounters, mostly olfactory, elicit responses that get it eventually to food, and eventually it picks up some food, and eventually it finds its way back inside.

What is contained in the notion that "being an ant," there are some things that the ant is likely to do? It has an ant's body, and that offers a set of possibilities for what it perceives, and how it moves, and what it can pick up. Maybe the joint actions of ants' bodies are likely to produce chambers with a certain curvature of the walls, because of the ways they move their heads as they scoop up sand. Being an ant also somehow establishes a set of possibilities for how ants respond to each other. We know that in many species of ants, individuals differ in their behavior, especially in how active or mobile they are. For some tasks, in some species, it has been shown that experience contributes to an ant's task performance.

The queen has a minimal role in organizing colony behavior. She does not direct the behavior of the ants in the colony. She has no authority. In fact, there is no evidence that any ant ever tells another what to do. So it would be absurd to imagine that somehow the queen carries inside her all of the instructions that later produce the behavior of the mature colony of ten thousand ants. A queen's life, after her brief, early excursion outside, consists of eating and laying eggs. In the laboratory, the queen of a large colony usually has some workers nearby. She rarely moves around much, and often seems to be standing doing nothing. Sometimes workers feed her, or groom her, or pile up eggs as she lays them. Winged reproductives are produced three to six weeks before the day of the mating flight, so a queen will have spent only a tiny portion of her life in her parent colony and will have little prior experience of life in a mature colony. She is outside of a nest for only a day or two to mate and get to the place where she will dig a new nest. Most newly mated queens die before they ever dig a nest; many are eaten by birds and lizards. If a newly mated queen does manage to start a nest, she digs furiously for the first two or three days, creating a single tunnel not much wider than her own body, about eighteen inches deep. She never comes out of the nest again, except if the colony moves to a new nest.

Apparently many new colonies do not survive, because there are many more nests of founding queens on the site each year (five hundred to one thousand) than there are one-year-old colonies the following year (twenty to fifty) (Gordon and Kulig 1996). I do not know if the queens die before they can produce any workers, or if the first batch of workers does not provide enough food to support the queen through the winter. Perhaps the small initial group of workers has a low probability of survival because there are not enough ants to compensate for each other's incompetence or to ensure that ants perform the necessary tasks. Maybe it often happens that the first few foragers out never find their way back; the probability of getting back to the nest may be low. In larger colonies, ants can use their foraging nestmates as a cue to the direction back to the nest, perhaps by following a gradient in the density of nestmates. But in a very small colony, a forager has a small chance of encountering a nestmate on the way home.

The accumulation of mistakes similar to those of the first foragers may prevent small colonies from successfully performing tasks inside the nest. In large colonies, some ants dig new chambers and others carry out the soil. The ants that scrape soil from the wall of the chamber might just put it down on the floor. Other ants walk by, and eventually some ant picks up a bit of soil and takes it somewhere else, maybe toward the entrance, maybe not. Eventually soil builds up near the entrance where ants pick it up and carry it out. In a very small colony, there may not be enough ants to ensure that on average, the soil will get out. Perhaps in some tiny new colonies, new chambers do not get built when they are needed. Small colonies may die because the chances of getting things done are low. But as a colony grows larger, eventually there comes a point when it has sufficient numbers of ants working in a sufficiently modified environment that on average, the colony accomplishes its tasks often enough to survive.

Colony Growth

Colonies grow quickly for the first four or five years (figure 12.1). If a colony manages to survive to be two years old, it will probably last out the next fifteen years (Gordon and Kulig 1998). A three- to four-year old colony, with four thousand to six thousand ants, is in the steepest portion of the colony's growth curve (Gordon 1992).

By five years of age, a colony can reach its mature size of ten thousand ants and begin to reproduce. This is a stable size; the colony ceases to grow, although, because ants live a year, all of its ants must be replaced each year. Colony growth may be limited by the queen's capacity to lay eggs; to maintain a size of ten thousand ants she must lay ten thousand eggs a year. A mature colony has an established nest mound and a set of three to eight habitual foraging directions, of which it chooses about two to five each day. It begins to reproduce, sending winged reproductives to the annual mating flight (Gordon 1992). It may remain in this state for another fifteen years.

Colonies vary in size. Some never seem to reach the size of the largest colonies (ten thousand to twelve thousand ants), and some never reproduce. Many of these apparently stunted colonies are in very crowded neighborhoods where competition for food may be especially intense. I suspect that such colonies do not reproduce because they are not large enough, perhaps because they do not have enough workers to collect sufficient reserves of food. However, there are also colonies that appear to be large but do not reproduce. We counted reproductives as they leave for the mating flight in two years and in both years, about a third of the colonies on the site that were of reproductive age did not send out any reproductives at all (Gordon and Wagner 1997; Wagner and Gordon 1999). If the colony reaches two years of age it is likely to survive for many years, but its development from ages two to five may determine whether it will reproduce.

Development of the Nest

The nest work of a small colony is different from that of a larger one, because the one-year-old colony is still making its nest, while the older colony is maintaining an existing nest. To construct a nest the ants have to kill any bushes growing where the nest is to be. They accomplish this by destroying the roots underground, and aboveground by climbing into the bush and clipping off the vegetation bit by bit. During the weeks of rainy weather that come each summer, the young colonies work on creating a nest entrance that will be raised above the level of the ground, which prevents water from pouring into the nest entrance. Using tiny twigs they make a thatched collar around the nest entrance, and then cover it with dirt.

When a colony is three years old it begins its period of most rapid growth, in numbers of ants. By this time most colonies have created a small nest mound. They have begun to cover the mound with tiny pebbles, which they bring in from the surrounding area. Any bushes remaining on the mound are dead, bare branches which eventually break off. There is usually a discrete pile or two of refuse, called the midden, with the husks of the seeds the ants are currently milling. Ants at work on the nest mound carry out sand from construction inside the nest, or sort and pile the midden.

When we dig up colonies, we find that there is a cone-shaped mass of chambers, with the top of the cone corresponding to the nest mound on the surface, and the length of the cone about the same as the diameter of the mound. A three-year-old colony's mound might be about half a meter wide, with a correspondingly deep cone of chambers; the chambers of a mature colony's nest may extend down one meter. Somewhere off the bottom of the cone is a single tunnel leading down another meter or even two, to a chamber where we find the queen and brood when we excavate a colony. These chambers can be as deep in a three-year-old colony as an older one. Probably the queen and brood do not usually stay so deep underground. It is clear the brood is not usually this deep, because on warm days it is easily found in chambers just underneath the top surface of the mound. In the laboratory, ants bring the brood to heated boxes, and the queen is usually near the smaller brood, eggs and small larvae. Perhaps in the field, the queen moves along with the brood as it is carried along a temperature gradient by the workers.

In excavated nests we find some chambers packed with stored seeds, and some with refuse. Colonies seem to use chambers and then build more as they are needed.

On the surface of the mound, the nest entrance has a smooth runway leading into it because the larger grains of dirt have been moved aside, leaving only the smallest ones. I can see a few centimeters into the nest with a fiber optics microscope. Inside the nest entrance of a three-year-old colony, the walls of the tunnels appear to be rough. In a colony of any age, there is a chamber just inside the nest entrance. In a three-year-old colony, that chamber usually divides into just two tunnels. Inside the nest of a colony five years or older, the walls of the chambers and tunnels seem smooth. The chamber nearest the nest entrance may branch into three or more main tunnels.

In a nest of any age, most chambers seem to have at least two openings, but some have more. I have never been able to trace the complicated topology of an entire nest. This topology is important, though, because the structure of the nest probably influences the flow of ants, and thus the rate at which ants interact as they come in and out of the nest.

Task Allocation

Task allocation of a mature colony, five years or older, differs from that of a small, young one in several ways (Gordon 1987, 1989a).

In a large colony, only about 25 percent of the colony works outside the nest, and large numbers remain inactive inside. These inactive ants may function as reserves that would emerge from the nest if needed in some situation. Such a situation has not occurred in the seventeen summers I have observed these ants, but though seventeen years is a long time for a person it is utterly insignificant on the evolutionary scale for an organism with a five-year generation time. In a young colony, a larger proportion of the colony, perhaps 50 percent, works outside the nest. Though the total numbers in the nest change with colony age as shown in figure 12.1, so that a six-year-old colony may be ten times as large as a one-year-old one, the numbers active outside the nest in a large colony are rarely more than two times those in a small one.

In the larger colony, ants in undisturbed colonies are unlikely to switch tasks from one day to the next. This suggests that an older colony has a larger number of ants available to perform exterior tasks than does a smaller one. In a small colony, an ant performing nest maintenance one day may be shunted into foraging the next. Perhaps in a large colony, an ant tends to be surrounded by more ants doing its own task, so there is a small probability it will encounter an opportunity to do a different task, or the stimulus provided by ants engaged in another task.

When the colony's environment changes, so do the numbers of ants engaged in the relevant task. If food appears, more ants forage. If the nest is disturbed, more ants take up nest maintenance and repair. These shifts lead to shifts in other, unrelated activities. I found in perturbation experiments that foraging, nest maintenance work, and patrolling are all related in this way: a shift in the numbers engaged in one task, caused by a change in the environment relevant to that task, leads to a change in the numbers engaged in the other tasks as well. These shifts arise from two ways that ants of one task respond to changes in the numbers performing another task: first, ants switch tasks, and second, ants may decide to become active, or remain inactive.

These adjustments in the distribution of workers performing colony tasks, differ in young and old colonies. The behavior of an older colony is more homeostatic, and more stable, than that of a younger one. The more a young colony is disturbed, the more it changes. However, the more an older colony is disturbed, the more its behavior seems to resemble that of an undisturbed colony. I do not know what process accounts for this result. Perhaps in a larger colony, each ant's behavior is somehow more buffered by the behavior of other ants.

The finding that small and large colonies differ in behavior suggests that the rate of interaction an ant experiences may influence its task. In an older, larger colony, an ant has more opportunities to interact than in a smaller one. If an ant's behavior is influenced by interaction rate, then even if ants act according to the same rules in small and large colonies, the outcome will differ. If an ant is likely to perform task X when it meets workers of task X at a certain rate, then large colonies may have more ants performing task X simply because each ant has more task X ants to meet. Such rules, of course, might involve positive or negative feedback. An ant's behavior is clearly subject to environmental influences as well as the influence of its interactions with others, but interactions seem to play a role in task allocation. For example, in laboratory studies we found that the probability an ant does midden work is correlated with the rate at which it encounters midden workers (Gordon and Mehdiabadi 1999). We also find that ants of different task groups differ in cuticular hydrocarbons, so that in the course of a brief antennal contact an ant can determine the task of the ant it meets. We are currently investigating how interaction rate contributes to task allocation, and we hope that this work will elucidate why old colonies appear to be more stable in behavior than younger ones.

Relations with Neighbors

Very small colonies differ from larger ones in their relations with their neighbors. I did some experiments in which I enclosed some colonies and observed the reactions of their neighbors (Gordon 1992). When a very young colony had its older, larger neighbor enclosed, its foraging trails would shift toward the foraging area of the absent neighbor. Neighbors of all ages reacted to the absence of an enclosed colony in this way. When the enclosed colony was released, the very young colonies left the foraging area of the newly released colony, and surprisingly, they retreated even more. A very young colony's foraging area after the neighbor was released, was even smaller than it had been before the experiment began. It was as though the sudden return of an absent neighbor was a stronger deterrent than that neighbor had been before it disappeared.

Colonies that are three to four years old, at the steep part of their growth curve, are more persistent in encounters with neighbors than younger or older colonies. When a colony were enclosed, its three- to four-year-old neighbors, like neighbors of other ages, began to use the foraging area of the enclosed colony. But when the enclosed colonies were released, the three- to four-year-olds, unlike smaller or larger colonies, did not leave their newly acquired foraging area. They returned to the site day after day, although this often involved fighting with the newly released colonies.

Colonies of five years or more seem to be much more staid in their relations with neighbors than the quickly growing three- to four-year-olds. When colonies were enclosed, older neighbors entered their foraging areas. When the enclosed colonies were released, the older neighbors simply retreated, foraging elsewhere much as they had before the enclosed colony disappeared. Older colonies adjust their foraging trails so as to avoid those of neighbors. Over the fifteen to twenty years of its life, a colony settles into relations with its neighbors. Ants distinguish nestmates from all other ants by a colony-specific odor. At least in harvester ants, workers also distinguish ants of neighboring colonies from ants of more distant, stranger colonies, presumably using the same colony-specific odor (Gordon 1989b).

Neighbor relations may change as colonies grow older because growth rates change. A three-year-old colony has four thousand workers to collect and process the food to make six thousand ants for the following year. By contrast, a six-year-old colony has ten thousand workers to collect and process the food to make a colony of the same size the following year. The larvae consume most of the food of the colony; adult ants eat much less. So in a young, growing colony, there are more hungry larvae per forager than in an older one that is larger but of stable size. In laboratory colonies there seems to be an increase in numbers foraging in the days following the appearance of larvae from eggs. This is the only direct evidence I have that the presence of larvae affects the behavior of foragers, but it seems clear this relation must be important. When there are no larvae, none are fed; when there are larvae, they are fed; somehow the behavior of foragers must be linked to that of the ants that feed larvae, and somehow that must be linked to the numbers of larvae present. Parts of this chain are understood for some social insect species, though we know little about the details in this species of harvester ant. Neighbor relations in the field are consistent with the speculation that a forager in a growing three- to four-year-old colony is under more pressure to obtain food than one in an older colony of stable size, because the ratio of brood to foragers is higher in the growing colony.

The relation between numbers of larvae to feed and the behavior of foragers is probably mediated in some way by the state of the colony's supply of stored food. Amount of stored food probably depends on colony size. I have excavated colonies of known age to count the ants, but have not been able to measure food stores accurately. My impression, though, is that older, larger colonies have larger food stores. In one colony of twelve thousand ants we found more than a liter of stored seeds.

Conclusion

Little is known about the development of social insect colonies, because there are few species in which individually labeled colonies have been followed over time. The work described here shows how much we have left to learn about the development of the behavior of a harvester ant colony. It seems plausible that many of the changes in behavior that we have observed arise from changes in colony size, which in turn lead to changes in the environment of the colony. Age-dependent changes in colony behavior seem to be a consequence of the relation between a colony's growth and its modification of its environment. This relation is complicated and not yet well understood. We do not know what determines the rate of colony growth. The availability of food, how well the colony collects and processes the food, the physiological condition of the queen, competitive pressure from neighbors, all are likely to influence colony growth. Colony size, in turn, determines how ants interact with each other, how many ants are available to collect and process food, and how a colony fares in competition with its neighbors. We know that all of these factors are related to colony size, though we do not yet know exactly how.

One set of important questions about colony development concerns the first few months of a colony's life. What do the first workers do? Why is colony mortality so high at this stage? Careful observation of very young colonies, both in the laboratory and in the field, would be very informative. A second set of questions concerns the relation between the physical structure of the nest, the flow of ants in and out of the nest, and the rate at which ants interact. Here both theoretical and empirical work is needed. Mathematical models of the complicated three-dimensional movement of ants through tunnels would help to guide empirical research. A third set of questions concerns the differences in task allocation in young and old colonies. Why is the behavior of older, larger colonies more stable and homeostatic than that of smaller, younger ones? Again, both theoretical and empirical work is needed. Models are needed that propose simple, plausible rules at the individual level, which might lead to the outcomes we observe in real colonies. Such rules determine how an ant's interactions, with its environment and with other ants, affects its decision about which task to perform. Differences between theoretical and empirical results show the gaps in our understanding, and point the way to further empirical work. A final set of questions concerns the relation between food and colony growth. We need to understand why some colonies grow faster than others. A colony's neighborhood influences its growth because neighbors compete for food; thus we need to know how food influences colony growth to understand how neighbors affect colony development.

The development of colony behavior is the process that relates changes in colony size to changes in the colony's environment. Each ant has the capacity to participate in this process, but that capacity is not separate from the process. An ant operates in the context of the colony. An ant alone could not function as an elemental unit of colony behavior, because there would be no colony behavior within which to act. As the colony grows, the ants encounter new circumstances. To our knowledge, an ant in a young colony responds to a particular situation in much the same way as an ant in an old one. But an ant in a young colony finds itself in different situations from an ant in an old one. An older colony is larger than a young one, and its environment has been modified by past cohorts of ants. To explain colony development we need to know how the behavior of mature colonies emerges from the changing relations of individual ants and their environment.

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