The Ant Colony's Dilemma

D. M. Gordon, Dept Biology, Stanford Univ.

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Harvester ants in the desert face a predicament that is becoming increasingly familiar to people around the world. Because of drought induced by climate change, cities are running out of water, crops are failing, and heat is making it dangerous for people to do the work needed to grow food. The deepening drought in the southwest US has created the same problems for the ants. Harvester ants eat seeds, mostly from grasses and flowering annuals, that are scattered by wind across the ground. A forager loses water to evaporation when it is out in the desert sun searching for seeds, while the ants get water from the fats in the seeds they eat. So the colony must spend water to obtain water and food. As the drought worsens, there are fewer plants to produce seeds, and the air is more dry, so it costs the colony more water to bring in food.

While drought imposes some similar constraints on how harvester ant colonies and people get food and water, we have many more options than the ants do. They can't move food or water around, or figure out how to share it, while we can. Whether this population of ant colonies survives will depend on how much and how fast the drought deepens, and how quickly evolution shapes the collective behavior that balances foraging and water loss. Whether a human population survives drought depends on similar biological constraints, but we can modify those constraints, because we can understand the problem and choose to respond. The ants show us, in microcosm, what happens when a population is threatened by environmental change and no one does anything about it. I hope that this outline of the ant colony's dilemma will stimulate discussion about parallels with human society.

Demography by ecologists

To show the problems faced by ant colonies in partitioning water resources, I will outline some of the results of two studies: first, an analysis of demographic and spatial data on a population of colonies (Sundaram et al 2022), and second, an analysis of differences among colonies in how they manage water loss (Gordon et al 2023). Since 1988 I have followed a population of about 300 harvester ant colonies per year in a patch of about 25 acres of desert scrubland in the valley of the Chiracahua Mountains. The site is just over the New Mexico side of the state line with Arizona, which runs about 50 miles south to the Mexican border. Each year we find the colonies that were alive the previous year, say goodbye to the ones that have died, and add the tiny new 1-year-olds to the map. During this time we have monitored about 1200 colonies through their life cycle.

Like any ecological study, this one investigates how and why populations change over time, in response to interactions with each other and the environment. I will use some familiar terms in the sense they are used by ecologists; in particular, individual, population, community and ecosystem. An *individual* can reproduce. A bacterium, a tree, a tiger, and a person are individuals in the ecological sense, although only individual bacteria can reproduce on their own; some trees, and all tigers and people, reproduce sexually, so it takes two individuals to make another one. A *population* is all of the individuals that actually do reproduce together; the spatial limit of the population is the range in which individuals interact. Thus a *species*, all of the individuals that could reproduce together if they were close enough, can consist of many discrete populations. A *community* is all of the populations, of different species, that are living together so as to use the same resources or use each other as resources. For example, every person is host to a community of many species of bacteria. Finally, an *ecosystem* includes both many communities of living organisms, and also the flow of resources and conditions that are not alive but influence the organisms, including water, air, and mineral nutrients.

The demography of a population depends on the rates of birth, death and emigration. *Recruitment* is the rate at which new colonies appear in the population; how long they live is *survival* or *mortality*.

The harvester ant colony life cycle

In social insects, the individuals are colonies in populations of colonies, because it is colonies that reproduce. Ants do not make more ants but colonies make more colonies: that is, colonies mate with other colonies to produce new offspring colonies.

A harvester ant colony is founded by one mated reproductive female, called a 'queen' though she does not direct the behavior of others. As in all ant species, the rest of the ants are sterile, female workers. A harvester ant queen leaves her parent nest in the first few weeks of her life to join a mating aggregation where she mates with many males. After the mating aggregation, the males die. The newly-mated queens fly off at random from the mating aggregation to found new offspring colonies. When the queen lands she detaches her wings, and if she is lucky enough not to get eaten by a bird or lizard, or attacked by another ant colony, she digs a hole. If she succeeds in producing a first batch of workers, and they manage to get enough food and water, by the next year there will be a new 1 year old colony. In fact only a small fraction of the female reproductives make it to start new colonies. But if she does, that queen can live for another 30 years, producing all of the workers, daughter queens, and male reproductives, using the sperm from her original mating session in the first few weeks of her life. Workers live only a year, so the queen must produce a new cohort each year, along with that year's reproductive offspring, who leave the nest each summer to mate. When the queen dies, there is no one to produce more workers, and the colony dwindles in size until all of the workers are gone and the colony is dead.

By tracking many colonies over time, I learned how quickly a colony grows from a single, mated queen. We excavated colonies of known age and counted all the ants. A 1-year old colony has hundreds of ants, grows rapidly in years 3 and 4, increasing to about 10,000 ants once the queen is 5. The colony stays at about that size for the remaining 25 years of its life. Figure 1 (Fig 1 from Sundaram et al 2022).

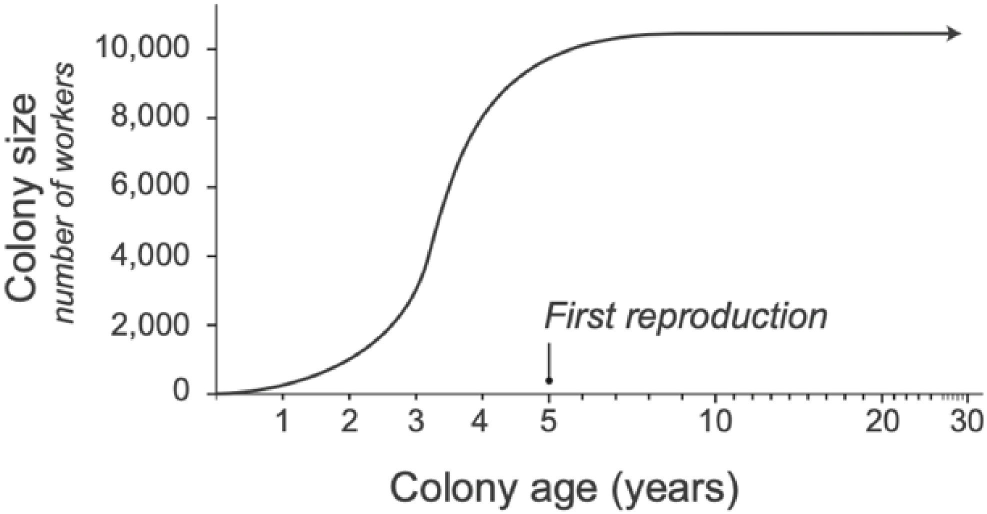

FIGURE 1 Colony life history. Colony size, in number of workers, as a function of the queen's age in years. All workers and reproductives are offspring of the single founding queen. Workers live only a year. A queen begins to produce reproductives for the annual mating aggregation at 5 years, and continues for the rest of her life

When a harvester ant colony reaches its mature size of about 10,000 workers, the queen begins to produce winged reproductives each summer. The colony sends out winged reproductives, both sons and daughter queens, who fly off to the mating aggregation where they mate with those of other colonies.

Because newly mated queens disperse at random from the mating aggregation, offspring colonies do not end up near their parents. We use genetic variation to identify which colony is the offspring of which parent colony. This makes it possible to measure a colony's lifetime reproductive success, as the number of offspring colonies founded over its lifetime by its daughter queens.

The collective regulation of foraging

Of the 15,000 known species of ants, only about 50 have been studied in detail. They all have in common that they operate without central control. Instead the allocation of effort to various tasks, including foraging, depends on local interactions among workers. (This perspective on task allocation regulated via interaction networks is outlined in Gordon 2010 and Gordon 2016). Interactions among ants are mostly olfactory, as ants have very poor vision but can distinguish hundreds of odors. Ants smell with their antennae and when one ant touches another, it smells the odor of a layer of grease on the other ant's body. Ants also detect pheromones, chemicals secreted by other ants.

Harvester ant colonies operate collectively to balance water loss against food brought in, adjusting their foraging activity to the current food supply and humidity. Foragers leave from, and return to, an entrance chamber linked by a short tunnel to the outside entrance of the nest. A returning forager drops its seed just inside the nest entrance, and then may go out again. This depends on its recent encounters with returning foragers. The forager will not leave the nest on its next trip unless it meets returning foragers with food at a high enough rate. This is a form of positive feedback. Within a day, each forager makes many trips. On each trip it keeps searching until it finds a seed, and once it finds a seed, it returns immediately to the nest. When there is more food outside, foragers find it and come back more quickly, so the rate at which foragers return, and meet outgoing ants, is a measure of the current food availability.

In this system, foraging is regulated without any spatial information. The seeds the ants collect are scattered by wind or flooding, and rarely in patches, so there is no use in directing more ants to a place where one ant has found a seed. In this way harvester ants are different from more opportunistic species, such as the ones that tend to show up in our kitchens, which use pheromone trails to recruit others to a particular location. By contrast, an encounter with a harvester ant forager returning from one direction can stimulate an outgoing forager to leave the nest traveling in another direction.

Thus for harvester ants, the regulation of foraging uses centralized rather than local information. All the exchange of information occurs with the nest. Such a centralized system is thorough, but slow, because a forager must leave the nest, search for a seed, find one and return to the nest before its success has any impact on the outgoing foragers. In other ant species, as in some human systems (e.g. Haber et al 2021), a more modular system allows rapid response to local changes (Gordon 2023).

However, for a harvester ant colony, thoroughness in searching is more important than speed, because the food supply changes slowly, on the timescale of days, not minutes, and a seed could be anywhere. The foraging activity of the colony is the aggregate of many forager decisions, which depend on a stochastic rate of return from foraging trips of varying duration, and the decision process of each ant is not fully deterministic either. The average foraging trip takes about 20 min at the peak of foraging activity.

Although the colony usually adjusts foraging slowly, they can respond more quickly. We did experiments in which we removed returning foragers and put them in a box (to be returned to the nest later). It takes only about 3 minutes for the flow of outgoing ants to stop, and it starts again as soon as the returning foragers are able to enter the nest for 2 minutes. This may allow them to respond to drastic events, such as their only predator, a horned lizard, standing alongside the trail and scooping up passing ants, but to resume foraging when the danger has passed.

A forager's decision to leave the nest on its next trip depends not only on food supply, but also on the on the humidity outside. The nest is a mass of adobe-lined chambers, open to the air only at the end of the tunnel from the nest chamber to the outside. An ant inside has no way to evaluate conditions outside, but a returning forager has experienced those conditions on its last trip. It seems that how desiccated an ant is when it returns influences its decision to leave again.

How often foragers go out, after they meet and smell each other in the entrance chamber, sets the foraging activity of the colony. The more willing a colony's foragers are to go out when stimulated by returning foragers, the more foraging gets done. In turn this determines how much food and water is available to be shared among the ants.

As climate change is raising the costs for colonies of foraging, it also affects their capacity to modify the environment so as to manage those costs. This may be analogous to the way that, in a human society, the costs of maintaining existing technology and the prospects for innovation depend on changing conditions. For harvester ants, the network of encounters between outgoing and returning foragers in the entrance chamber is the valve that regulates water loss. As the drought has deepened, the soil has dried out. In extreme heat the upper layers of soil turn to dust, sometimes caving in and opening the ceiling of entrance chamber and others near the surface of the mound. Then the ants are exposed to the dry outside air, and can't regulate how much they go out until they can rebuild the entrance chamber. Normally the ants line the chambers with moist soil that dries to an adobe finish that helps retain moisture - but it's not possible to make adobe out of dust. Some colonies try making new entrances in firmer, moister soil, others dig deeper and wait inside the nest for rain. But the ants do not have the capacity to develop innovative new ways to regulate the humidity inside the nest. Again, there may be interesting parallels with the ways that human societies attempt to maintain existing technology, for example in agriculture, in changing conditions.

Variation among colonies in the regulation of foraging

All colonies have to manage the tradeoff between water loss and food supply, and all the colonies in the population are experiencing the same drought conditions. But colonies differ in how they manage this (Gordon et al. 2023). When it's overcast and humid, or the day after rain, the decision is easy and all colonies react in the same way. It is easier to obtain food when it is humid because an ant can walk around searching for seeds without losing much water. After a rain, the upper layer of the soil is washed away, exposing more seeds for the ants to find. So on the day after rain, during the summer monsoon season when plants are flowering and setting seed, it's a foraging extravaganza, with ants pouring out of all the nests and streaming back in with seeds.

When it's dry outside there is more at stake. If there hasn't been much rain, there might not be much food, and the drier the air, the more water will be lost by ants outside searching. Is it worth it to go out on the next trip?

Colonies differ in how much they forage on dry days, when the risk of water loss is high. In some colonies, the foragers make fewer trips on dry days, reducing overall activity and thus sacrificing food intake. In these colonies, a forager is less likely to leave the nest, in response to encounters with returning foragers, when conditions outside on its last trip were dry. The colony lives off of stored food and conserves the water that would be lost while searching. But in other colonies, the foragers keep making many trips on dry days, despite the water loss, so that foraging activity remains high. We found that within a colony, foragers are similar in their assessment of when it is too dry to leave the nest, indicating these differences among colonies are colony-wide, not due to differences among colonies in the distribution of forager assessment of humidity conditions (Nova et al 2022).

We measured foraging activity in the same colonies year after year. First, in each year we compared the numbers foraging on the driest and most humid days of each year, and characterized a colony as one that reduces foraging on dry days if its activity was reduced by at least 20% on dry days relative to humid ones. We then found that the same colonies tend to reduce foraging year after year.

These differences among colonies are apparent only on dry days. The figure below compares the foraging activity of two sets of colonies, those that consistently reduced foraging on dry days, and those that never did. Foraging activity was significantly different in the two groups of colonies only on dry days.

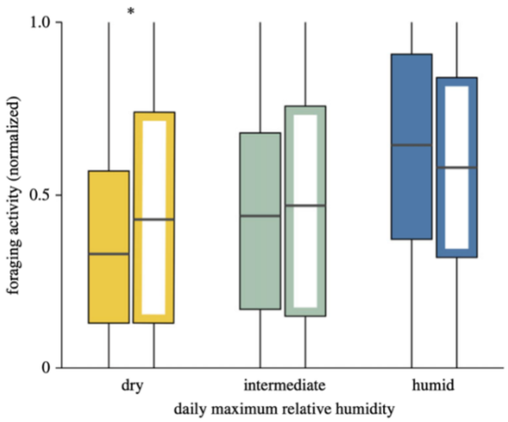

Figure 6. Comparison of foraging response to humidity level in colonies that reduce foraging on dry days and those that do not. Each bar represents the foraging activity, normalized for colony size as the proportion of the largest number of ants seen foraging in that colony in that year, on all days in all years with the indicated humidity level. Filled bars represent colonies that consistently reduce foraging on dry days; open bars represent colonies that do not. * = $p < 0.05$, Wilcoxon sign ranks test.

Fig. 5 (Fig. 6 from Gordon et al. 2023)

Natural selection can shape this variation among colonies in how they manages water loss when the collective regulation of foraging is heritable, and when it influences colony survival and reproduction. This is selection on variation among colonies in how much a colony forages on dry days, which is the outcome of many foragers' decisions whether to leave the nest on the next trip in response to interactions with returning foragers. To learn how this is evolving in the population over generations of colonies, we are investigating the physiological differences among colonies that determine how foragers respond to interactions, and how these differences might be inherited from parent to offspring colonies.

One reason colonies differ in foraging decisions is in the chemistry of the waxy layer, called cuticular hydrocarbons, that coats the ants' bodies and keeps them from drying out. Ants in the colonies that forage less in dry conditions lose water faster than the ants of colonies that keep foraging no matter what. A second physiological process that influences a forager's decision whether to leave the nest on its next trip is mediated by dopamine in the ant's brain. We found genetic differences among colonies related to the metabolism of dopamine. Then we fed foragers dopamine, and the foragers with higher dopamine levels made more foraging trips. Dopamine is associated with risk and reward in many animals. For harvester ants, dopamine seems override a forager's sense of risk, that it was way too dry on its last trip to warrant going out again. In colonies with less waterproofing and less dopamine, foragers come back to the nest more dehydrated and less willing to go out again on another trip, and so overall, the colony forages less.

It seems likely that these differences among colonies, in the chemistry of the waxy outer layer that prevents water loss, and in the neurophysiology of dopamine, are heritable from parent to offspring colony. One line of evidence for this is that colonies show similar behavior year after year (Gordon et al. 2023), while the ants live only a year, so one cohort of workers apparently inherits the same physiology as the next cohort from the queen. However, we are now working to look at this explicitly by comparing the behavior of parent and offspring colonies.

If colony differences are heritable, and influence a colony's chances of producing offspring colonies, then natural selection can act to shift how colonies regulate foraging to manage water loss. If so, the question is whether natural selection can act quickly enough to keep up with the rate of climate change. The rate of natural selection is set by generation time, which in this species is 5 years. In principle the rate at which a human society could adjust is much faster, as we could change behavior within a generation rather than waiting for the slower pace of natural selection over many generations.

Dealing with the neighbors

A harvester ant colony lives in a neighborhood of other harvester ant colonies. While this there are many other ant species in the same area, for this species there is generally more competition with others of the same species than with other species who rely on different food sources. Most harvester ant colonies have several neighbors of the same species within about 10 meters. They all compete for foraging area. Because the seeds that the ants eat are scattered by wind and flooding, the food supply from any place is as good as the food from any other. Every bit of foraging area has equal value. The plants whose seeds the ants eat are annual, distributed differently each year, so no location has a predictably superior supply over the lifetime of a colony. Thus the more area a colony can search, the more food the ants are likely to bring back.

Neighboring colonies compete because their foraging areas can overlap. Often the foragers of neighboring colonies meet as trails from each colony's nest lead them to search in the same area. Fighting is rare, usually restricted to the days after a rain when foragers can afford to be out longer. (As Josh Ober suggested, the necessity to focus on the harvest may have similarly constrained the seasonal timing of wars among ancient Greek city-states). Fighting can go on for a long time: one ant grabs onto another with its mandibles and attempts to rip its abdomen from its thorax - but rarely succeeds. Often the attacking ant dies of desiccation, and its body breaks off but its mandibles stay clamped on, so the other ant spends the rest of its life with the head of its attacker attached. The main cost of overlap in the foraging areas of neighboring colonies is in food, not in ants lost to fighting. Whatever food one colony takes, the other has lost.

The relations among neighboring colonies change as colonies grow older and larger. Although ants live only a year, a colony's behavior depends on its size and growth rate. Adolescent colonies, just before they get ready to reproduce, make obnoxious neighbors, returning day after day to a place where it met the foragers of a neighbor. Most of an ant's food goes to feed the larvae. An adolescent colony is growing quickly, so the ratio of larvae needing food, to foragers available to get it, is very high. A 3-year-old colony with 4,000 ants needs to make 6000 ants for the following year. This pressure seems to push the foragers to keep searching even if they meet the neighbors. Very small, young colonies are wimps, with foragers likely to retreat when they run into neighbors. Older colonies tend to direct their trails away from a location where they met a neighbor, which over time diminishes the amount of overlap.

Like trees in a forest where shade from large trees slows the growth of younger, smaller ones, a small colony surrounded by large neighbors is not likely to find somewhere to forage that its neighbors have not already searched. Ultimately, the colony may not survive. Colonies founded near other small ones form neighborhoods of colonies of similar age, who then have to partition foraging area throughout their 20-30 year lifetimes.

Colonies in crowded neighborhoods have smaller foraging areas. We found that as a result, the more crowded a colony, the less likely it is to survive (Sundaram et al. 2022). We used the census data from 1988 to 2019, with the locations and ages of about 1200 colonies, to ask how the spatial distribution of the neighborhood influences whether new colonies can join it, and whether the existing colonies survive (Sundaram et al. 2022). As a measure of a colony's foraging area, we used Voronoi tessellations to generate a polygon around the location of each colony's nest. This draws the smallest polygons that can separate an array of points, and captures the observation that one colony's trail never crosses a trail of another colony. The first use of this tessellation was by John Snow in the London cholera outbreak of 1855. He used it to map cholera infections in relation to the nearest well for each household, and show that cholera was spread through drinking water.

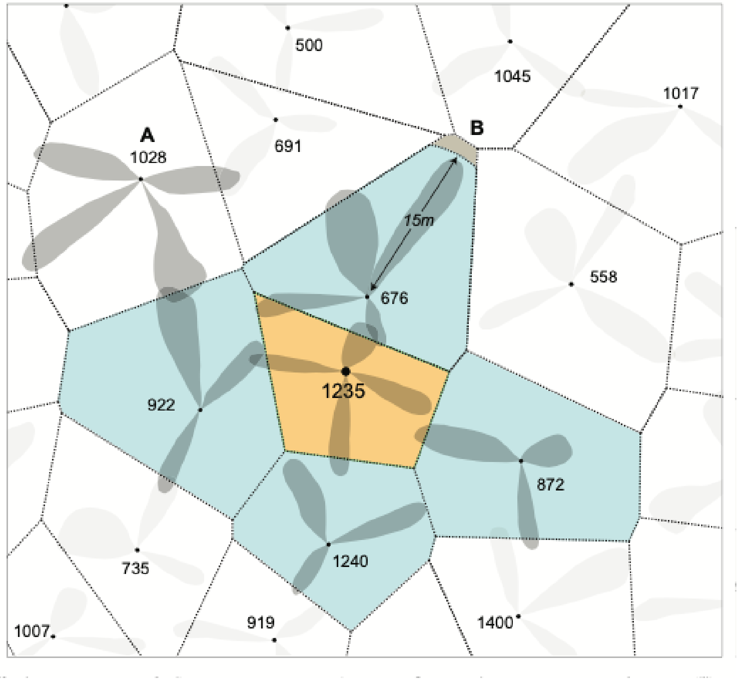

FIGURE 6 Illustration of Voronoi tessellation to identify neighbors and estimate foraging area. Black dots show the locations of the nests of the indicated colonies. Dotted lines show the outlines of Voronoi areas. The shaded gray shapes illustrate hypothetical foraging trails, taken from maps of foraging trails of other colonies. The arrow extending from 676 shows 15 m; the shaded area near B shows the part of the Voronoi area past 15 m from the nest that was eliminated in estimating modified Voronoi areas. All the colonies with areas shaded blue are neighbors of colony 1235 whose area is shaded yellow, because they share an edge of their respective Voronoi areas with colony 1235. Colony 1028 at A is not a neighbor of 1235, although its nest is close to that of 1235, because the Voronoi area of 1028 does not share an edge with the Voronoi area of 1235. This reflects the low probability that the foraging trails of colony 1028 would ever meet those of 1235 because of the barrier formed by the foraging trails of 1235's neighbors 922 and 676

Figure 2 (Fig 6 in Sundaram et al 2022)

We performed logistic regressions to ask how colony survival depends on the following variables: age class (young [1–2 years], teen [3–4 years], young adult [5–10 years], adult [11–17 years], old [18 years or older], Voronoi area, modified Voronoi area, average modified Voronoi area of neighbors, the propor- tion of neighbors in each age class, area of neighbors, distance to the nearest neighbor, summer precipitation, summer precipitation from the previous year, annual precipitation, and annual precipitation from the previous year (see Table 1 in Sundaram et al 2022).

We used simulations to compare the observed distribution of new nests with a random distribution of new nests, to see how the probability that a new nest could survive depended on the spatial configuration of the neighbors.

The results show that a colony's chances of surviving to the next year depend on its age and on the foraging area available in its local neighborhood. Recruitment, a founding colony's chance of surviving to be 1 year old, has changed over time with the decrease in rainfall. When rainfall was high in the first 14 years of the study, colony numbers increased, and then began to decline after about 1997–1999, apparently due to crowding. As rainfall decreased, beginning in about 2001–2003, fewer new colonies have become established. Less rainfall means fewer flowers that produce fewer seeds. As rainfall has declined and food has become more scarce, it takes a larger foraging area to support a colony. Colonies are dying younger and fewer new ones are surviving. Thus while all colonies now have more space than they did in during the early years of the study when there was abundant rainfall, there is less food available now than there was. As a result, a colony requires more foraging area to survive. A neighborhood that was spacious in 1998 is crowded now. These trends are shown in the figures below, Figs 2,4, and 5 from Sundaram et al. (2022).

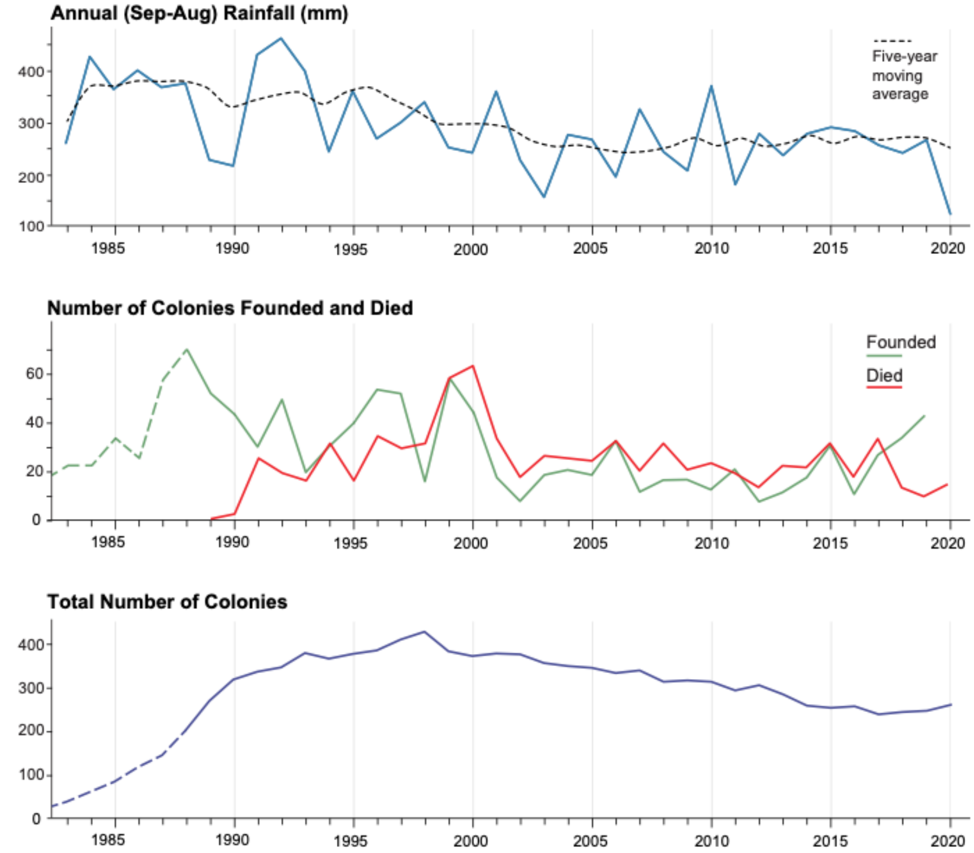

FIGURE 2 Annual rainfall, number of colonies that were founded and number that died, and the total number of colonies. The dashed line in the top figure shows annual rainfall as a 5-year moving average, and the solid line shows the annual values. In the lower two figures, dotted lines before 1988 show extrapolated number of colonies founded and extrapolated total numbers; when the census began in 1988, all colonies with nest mounds as large as those of colonies known to be five were considered to be 5 years old, although they may have been older

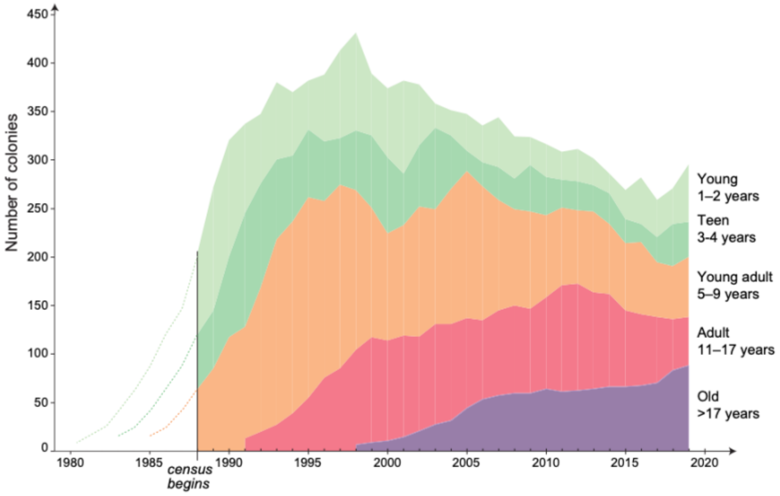

FIGURE 4 Change in population age structure over time. Each color shows the number of colonies of the indicated age. Dotted lines before 1988 show extrapolated ages; when the census began in 1988, all colonies with nest mounds as large as those of colonies known to be five were considered to be 5 years old, although they may have been older. Dotted lines approaching 2019 reflect the 2 year lag for inactivity before colonies are determined to have died

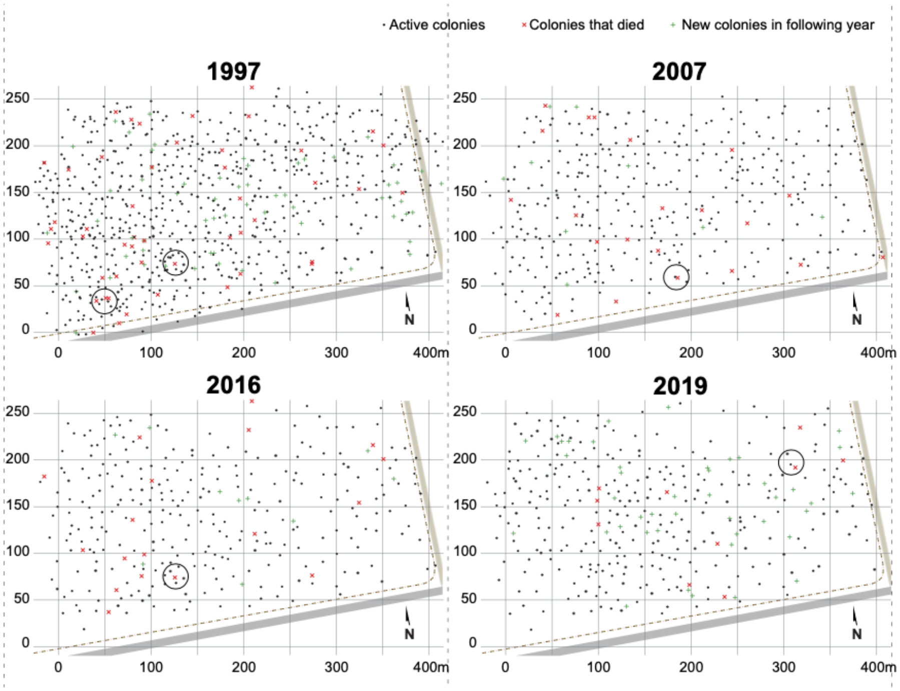

FIGURE 5 Maps of the colonies at the study site for 1997, 2007, 2016, and 2019. The gray stripe indicates a road along the southern edge of the site, and another road built in 2001 along the eastern edge. Maps are shown for 1997, when the number of colonies was high (see Figure 2); 2007, after numbers began to decline; 2016, when the number of colonies was low; and 2019, when the number of colonies may be rising. Black dots show colonies active in the indicated year; a red × shows a colony that was active in the indicated year but dead by the following year, and a blue plus sign shows the location of a new colony the following year. In each map, one colony is shown surrounded by a circle to provide an example of a colony with a small foraging area that was dead the following year (red ×), and its neighbors (black dots)

The ant colony's dilemma

The population of harvester ant colonies is a mosaic of neighborhoods, consisting of colonies that differ in how they manage water. Long-standing relations among neighboring colonies, continuing over decades, determine whether a colony can survive. Each colony's chances of survival depend on how its way of dealing with dry days plays out in relation to that of its neighbors. If a colony that saves water and forages less on dry days is surrounded by neighbors that don't, on dry days it will lose all the food to the neighbors. But if all the colonies in a neighborhood are restrained enough to reduce foraging on dry days, all will do better. By contrast, if all the colonies in the neighborhood spread out to search for food regardless of the weather, on dry days as well as humid ones, the foraging area of each one is set by how far ants of one colony can go before they meet the others. Neighborhoods are likely to have a mix of colonies that differ in foraging behavior. This situation has some resemblance to the prisoner's dilemma, but an ant colony cannot make any predictions about the behavior of its neighbors.

As climate change hurtles forward, will the ants make it? This depends on how much and how fast the drought deepens, but also on how the population evolves over generations of colonies. A few years into the current drought, in 2010, we found that colonies that conserved water were more likely to have offspring colonies (Gordon 2013). We are now asking whether natural selection still favors restraint by the colonies that reduce foraging in dry conditions. Natural selection can shape collective behavior only through the way that individual foragers respond to encounters, by acting on variation among colonies in their foragers' decisions whether to leave the nest on another trip, in dry conditions. If the drought gets worse quickly, the food supply may decrease so much that a colony can't afford to sacrifice food, even to save water, especially if it is in a neighborhood of colonies that keep foraging no matter how harsh the weather.

The evolutionary question about the harvester ants is the same one that we are asking about plants and animals everywhere, including ourselves: can they evolve fast enough to deal with what comes next? The question for us is whether our own collective behavior and technology can change quickly enough, so as to respond to, and modify, the environment in ways that permit us to survive and even flourish.

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