

ARTICLE

Rainfall, neighbors, and foraging: The dynamics of a population of red harvester ant colonies 1988–2019

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Handling Editor: Katharine L. Stuble

Abstract

Changing climatic conditions are shaping how density mediates resource competition. Colonies of the seed-eating red harvester ant, *Pogonomyrmex barbatus*, live for about 30 years in desert grassland. They compete with conspecific neighbors for foraging area in which to search for seeds. This study draws on a long-term census of a population of about 300 colonies from 1988 to 2019 at a site near Rodeo, New Mexico, USA. Rainfall was high in the first decade of the study, and then declined as a severe drought began in about 2001–2003. We examine the effects on colony survival and recruitment of the spatial configuration of the local neighborhood of conspecific neighbors, using Voronoi polygons as a measure of a colony's foraging area, and consider how changing rainfall influences the effects of local neighborhoods. 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, measured as a founding colony's chance of surviving to be 1 year old, depends on rainfall. In the earlier years of the study, when rainfall was high, colony numbers increased, and then began to decline after about 1997–1999, apparently due to crowding. As rainfall decreased, beginning in about 2001–2003, recruitment declined, and so did colony survival, leading to a trend toward earlier colony death which was most pronounced in 2016. As rainfall declined, apparently decreasing food availability, more foraging area was needed to sustain a colony: although the number of colonies declined, the impact of crowding by intraspecific neighbors increased. These processes maintain overdispersion on the scale of about 8 m, with transient clustering at larger spatial scales. In addition, other factors besides crowding, such as the colony's regulation of foraging activity to manage water loss, appear to contribute to a colony's survival. The adaptive capacity for selection on the collective behavior that regulates foraging activity may determine how the population responds to ongoing climate change and drought.

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KEYWORDS

adaptive capacity, climate change, competition, density dependence, drought, spatial distribution

INTRODUCTION

A basic question in ecology is how density regulates population dynamics (Turchin, 1995). The spatial distributions of sessile organisms can reflect the outcome of competition for a resource bounded in space (Krebs, 1999). Density shapes local interactions in spatial neighborhoods. These interactions influence recruitment, growth, and mortality by creating the spatial patterns of local neighborhoods. Changing climatic conditions can shift the effects of density dependence on resource competition (Acker et al., 2020; Jaatinen et al., 2020; Santora et al., 2020).

In plants and sessile animals, competition among neighbors for a spatial resource can produce overdispersion and other self-organized patterns (Brisson & Reynolds, 1994; Deblauwe et al., 2011; Dong, 2020; Dukas & Edelman-Keshet, 1998; Getzin et al., 2016). The processes that generate spatial distributions often involve scale-dependent feedback (Rietkerk & van de Koppel, 2008; Zhao et al., 2019), in which both the intensity and the direction of interactions among neighbors depend on distance. Behavioral interactions among neighbors produce spatial patterns at every biological scale from cells (Halatek et al., 2018) to animals (De Paoli et al., 2017). While scale-dependent feedback has mostly been studied in plants, in animals it can result from territorial behavior (Adams, 2001; Pringle & Tarnita, 2017) and other interactions among neighbors that lead to space partitioning (Huxley, 1934; Lewis et al., 1997; Lewis & Murray, 1993; Santora et al., 2020; Stamps & Krishnan, 2001). Since territorial behavior constrains the possibilities for reproduction, its effects on spatial distributions influence population dynamics (Gordon, 1997; Morales et al., 2010).

Social insect colonies in many species are sessile organisms, remaining in one place throughout the colony's lifespan. They provide a compelling system in which to examine how resource competition can determine spatial distributions (Adams, 2001; Levings & Traniello, 1981; Ryti & Case, 1986) and how the effects of neighbors on survival and reproductive success shape population dynamics. In ant communities, competition among neighboring colonies influences the spatial distributions of coexisting species (McGlenn et al., 2021; Perfecto & Vandermeer, 2013; Tanner & Keller, 2012). In many ant species, intraspecific competition for foraging

area influences population dynamics (Adams, 1998; Adams & Tschinkel, 2001; Boulay et al., 2007; Boulay et al., 2010; Chen et al., 2018; Cushman et al., 1988; Elmes, 1974; Korzukhin & Porter, 1994; Lorinczi, 2011; Yamaguchi, 1995). Seed-eating harvester ants in sagebrush and desert chaparral of the western United States have provided opportunities to learn how competition influences spatial distributions (Crist & Wiens, 1996; Dibner et al., 2015; Robertson & Robertson, 2020; Ryti & Case, 1986; Wiernasz & Cole, 1995).

Spatial distributions structured by resource competition are strongly influenced by variation among individuals in the intensity of resource use (Tarnita et al., 2017). For example, resource competition is mediated by life history (Brandl et al., 2018; De Cubber et al., 2018), which can influence how competition generates spatial patterns (Pringle & Tarnita, 2017). Sessile organisms, such as trees and some species of ants, tend to collect more resources as they grow older and larger; for example, light in the case of trees, and food in the case of ants (López et al., 1994). Moreover, individuals, even of the same life history stage, may vary in behavior that influences resource use, with important effects on intraspecific competition (Anderson et al., 2011; Lott, 1991). Ant colony's resource use also changes, as a colony grows older and larger (Ryti & Case, 1992).

Competition for resources is mediated by changing conditions that influence resource availability. Increasingly severe and frequent drought is a widespread consequence of climate change (Pearson & Dawson, 2003), likely to have important effects on species distributions (Cady et al., 2019). Here, we examine how life history and long-term changes in climate, especially rainfall, influence the effect of spatial neighborhoods on the dynamics of a population of colonies of the red harvester ant, *Pogonomyrmex barbatus*.

The study system

Our study used data from 1988 to 2019 from a census, conducted each year since 1988, of a population of colonies of *P. barbatus*, at a 10-ha site near Rodeo NM. The site has been occupied by about 300 colonies each year, for a total of 1057 unique colonies identified and monitored, with age and location known, between 1998 and 2019.

Colony life cycle

A *P. barbatus* colony consists of one female reproductive, the queen, and many sterile female workers. The census and genetic studies have shown that a colony lives for 20–30 years, founded by a single queen (Gordon, 1992a; Gordon & Kulig, 1998). The queen produces all of the ants in the colony (Suni & Gordon, 2010), including workers and reproductive males and females, using sperm obtained by mating with many males. Excavations of colonies of known age (Gordon, 1992a) show how colony size changes with colony age (Figure 1). When the queen is about five years old (Gordon, 1995), the colony begins to produce reproductives, winged males and females, both from eggs laid by the queen, that join an annual mating aggregation. After mating, the males die, and the newly mated queens fly off at random from the mating aggregation (Ingram et al., 2013) to find new colonies. When the queen dies, and all the workers have died, the colony is dead; the colony does not adopt a new queen.

At the yearly mating aggregations, there can be thousands of reproductives, up to about 200 for each of the 100–200 colonies that participate (Gordon & Wagner, 1997; Wagner & Gordon, 1999). Dispersal distances are about 70 m, within the spatial scale of the study site, which is about 250 × 450 m, so most parent and offspring colonies are within the site (Ingram et al., 2013; Suni & Gordon, 2010). Each year after the mating flight, there are many hundreds of nests created by newly mated queens (personal observation), but very few of these, 10–50, survive until the following year to be 1-year-old colonies (Figure 2). Here, we ask what affects the probability that a founding colony, created by a newly mated queen, survives to be 1 year old.

Like many populations in the genus *Pogonomyrmex*, this one has two dependent but not interbreeding genetic



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

lineages (Cahan & Keller, 2003; Volny & Gordon, 2002). A queen must mate with at least one male of each lineage to produce a viable and reproductive colony, because matings between a queen and a male of the same lineage produce female reproductives, while matings between a queen and a male of the other lineage produce sterile female workers. In previous work, we found no ecological advantage in colony survival, or differences in colony behavior, associated with the lineage of the queen (Gordon, Pilko, et al., 2013). In this population, as in others, one lineage is consistently more abundant than the other, and it appears that the asymmetrical lineage ratio arises from differences between the two lineages in sex ratio.

In a previous study, we used microsatellite variation to identify mother–daughter pairs of colonies among 258 colonies, aged 1–28 years, in 2010 (Ingram et al., 2013). This made it possible to construct a life table for the population. Only about 25% of the mature colonies evaluated in that study had ever reproduced offspring colonies, that is, colonies founded by a daughter queen of the parent colony, in their lifetimes so far. The number of offspring colonies ranged from 1 to 8. There is no evidence for reproductive senescence; a colony can continue to produce reproductives, and thus offspring colonies, until its queen dies.

Microhabitat and vegetation

There was grazing by cattle at the site until 1993–1994, and some occasional further grazing until 2000 when the site was fenced. Vegetation cover and species composition vary greatly across the site and from year to year (Figure 3), apparently linked to rainfall. Most of the seeds collected by the ants are from annual plants. Many are scattered by wind and flooding, and do not come from vegetation growing on the site; at times foragers collect as many seeds from the bare ground as from densely vegetated areas (Gordon, 1993), while at other times the ants collect seeds from nearby plants. The distribution of plants changes so much from year to year that there is no evidence for any consistent year-to-year effect of nest location on seed availability. Thus, neighboring colonies compete for the use of any foraging area in which to collect whatever seeds have arrived there, not for the use of particular locations with vegetation that persistently provides seeds.

Other granivorous ant species

Competition with conspecifics is apparently much stronger than with other species. The other *Pogonomyrmex*

species that has been consistently present at the site is *P. desertorum*, with at most 10–15 colonies found on the site in a given year, and rarely in the same location as the previous year. The ants of this species, like the other seed-eating ant species at the site, such as *Pheidole desertorum*, are much smaller and so forage for much smaller seeds (Chew, 1976; Davidson, 1977a, 1977b, 1980; Whitford, 1978; Whitford et al., 1976). Early in the study, there were a small number of colonies of other *Pogonomyrmex* species with large ants. First, there were a few *P. rugosus* colonies through the early 90's, but they

then disappeared, both from the site and from the other side of the road, where they had been more abundant. There have also occasionally been colonies of *P. maricopa* and possibly *P. californicus* (Gordon, 1984) at the site, but since the early 2000's there have never been more than two *P. maricopa* colonies on the site in any year.

There are several ant species at the site that are large enough to collect the same size seeds as *P. barbatus*: *Myrmecocystus mimicus*, *M. mexicanus*, and *Novomessor cockerelli* (during the course of this study, *N. cockerelli*

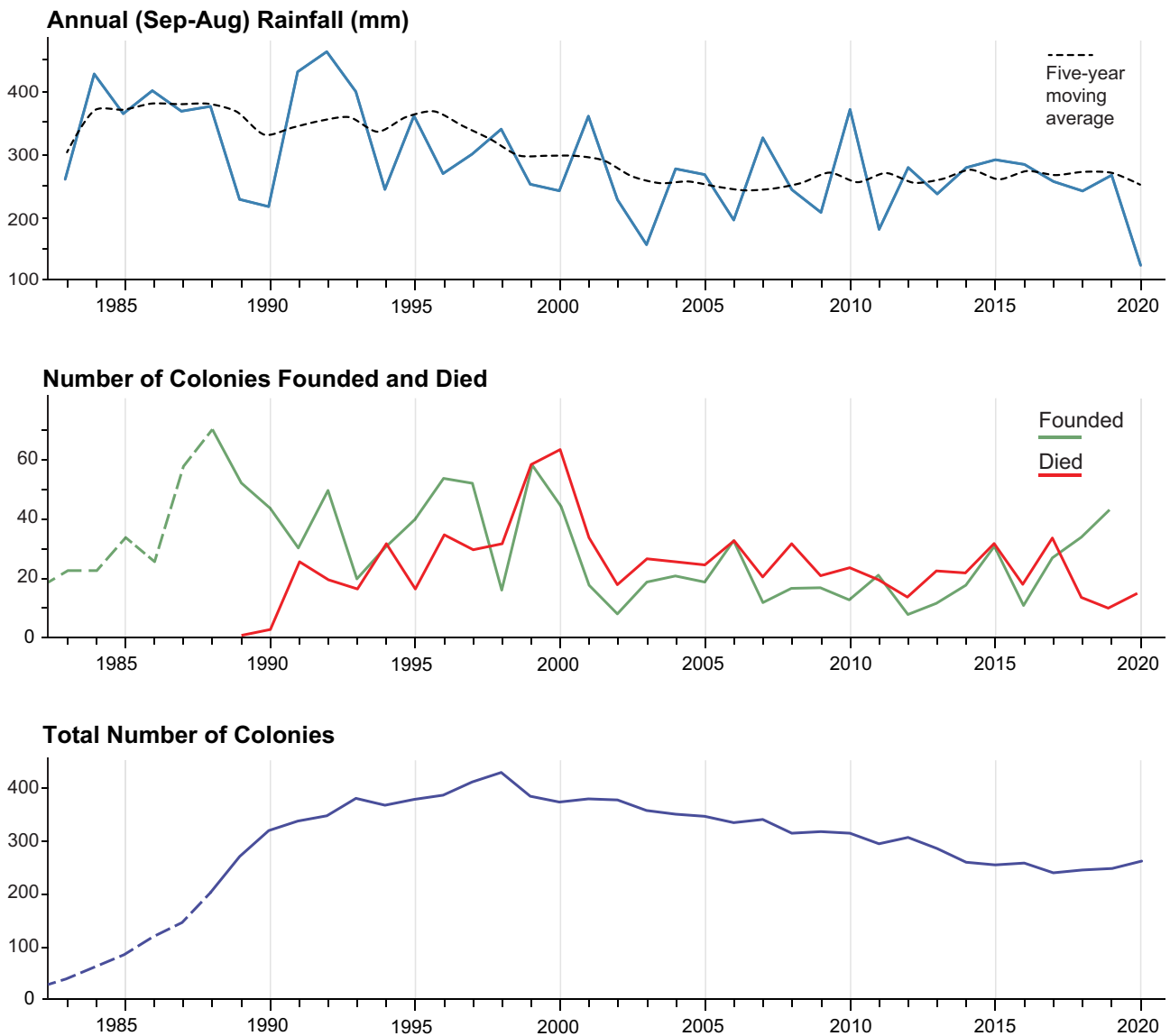


FIGURE 2 Annual rainfall, number of colonies that were founded and number that died, and the total number of colonies. The dashed line in the top figure shows annual rainfall as a 5-year moving average, and the solid line shows the annual values. In the lower two figures, dotted lines before 1988 show 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 3 Photos. The photo on the top left shows the nest mound of a mature colony, 5 years or older. A cleared foraging trail is indicated with an arrow to the upper right of the photo. The photo on the top right shows foragers traveling toward and away from the nest entrance. The two photos on the bottom illustrate the difference in vegetation when there is more (left) or less (right) rainfall

was renamed *Aphaenogaster cockerelli* and then again *N. cockerelli*). Unlike *P. barbatus*, all three of these species collect arthropods as well as seeds. *Myrmecocystus mexicanus* is rare on the site; the largest number of colonies ever found on the site was 10 in 2000. Colonies of *M. mimicus* were abundant on the site in the late 90's, but numbers declined sharply beginning in 2001: of 70 colonies marked in 1999, only 29 (41%) were still active in 2003, and only 6 (8%) were present in 2004.

Novomessor cockerelli forages at night for both seeds and arthropods. While they rarely forage at the same time as *P. barbatus*, the two species do interact, because *N. cockerelli* sometimes plugs the nests of *P. barbatus* colonies at night (Gordon, 1988), especially the nests of small, young colonies (Barton et al., 2002). Nest plugging by *N. cockerelli* delays the time that the *P. barbatus* colony emerges because it remains dark inside the plugged nest when the morning light reaches open nests and

stimulates the onset of foraging. Eventually the *P. barbatus* colony digs its way out, but since its foraging activity is inhibited by the midday heat, the result of the delay is that its foraging activity has been cut short, thus leaving more seeds available for the *N. cockerelli* colony that night.

The abundance of *N. cockerelli* declined sharply during the course of this study. They were abundant on the site beginning in about 1997 and began to decline in about 2003 or 2004. Of 55 colonies mapped in 2000, most with more than one nest mound, 41 (75%) were active in 2003 and 20 (35%) in 2004. Before 2007, there appeared to be some competition for nest sites with *P. barbatus*, as both species have occupied the abandoned nests of the other (personal observation). However, for unknown reasons, the population of *N. cockerelli* colonies declined rapidly after 2005 and then disappeared; they were absent from the site between 2008 and 2012. A few colonies

appeared on the site in 2013 and there have been 3–5 active nests each year since then.

Here, we do not consider how the spatial distributions of either *M. mimicus* or *N. cockerelli* influence the spatial distribution of *P. barbatus* in the long term. It is not known how long colonies of *M. mimicus* and *N. cockerelli* survive, but their colony lifespan may be much shorter than that of *P. barbatus*; at least their nest sites change on a much more rapid timescale than the lifespan of a *P. barbatus* colony. As the abundance of both species began to decrease sharply at about the same time as the numbers of *P. barbatus* colonies began to decline slowly (Figure 2), it seems unlikely that competition with either species had a strong impact on the survival and recruitment of *P. barbatus* colonies.

Rainfall

Red harvester ant colonies compete with conspecific neighbors for food. Resource competition has also been demonstrated in other *Pogonomyrmex* species, *P. californicus* and *P. occidentalis*, in both observational (Cole & Wiernasz,

2002; De Vita, 1979; Fewell, 1988; Harrison & Gentry, 1981; Wiernasz & Cole, 1995) and experimental studies (Billick et al., 2004; Ryti & Case, 1986). In *P. barbatus*, both foraging activity and interactions with neighboring colonies change over a colony's life history, as colonies grow from the founding stage, increase rapidly in size and then become reproductively mature (Gordon, 1992a; Gordon & Kulig, 1996).

About 60% of the annual rainfall in the Lower Sonoran Desert occurs during the summer monsoon season; the rest is mostly during the winter (Mullen et al., 1998). Over the course of the study period, 1988–2019, rainfall increased and then began to decline in about 2001–2003 (Figure 2). The study period spans first the highest rainfall and then the most severe drought in the southwestern United States in the past 1000 years (Williams et al., 2020). Both mortality and recruitment of new colonies have changed (Figure 2), and this is reflected in changes in the age structure of the population (Figure 4).

Rainfall is likely to affect competition for food in red harvester ants in two ways. First, food availability is probably closely linked to rainfall. Red harvester ants feed on seeds, mostly of desert annual grasses (Gordon, 1993),

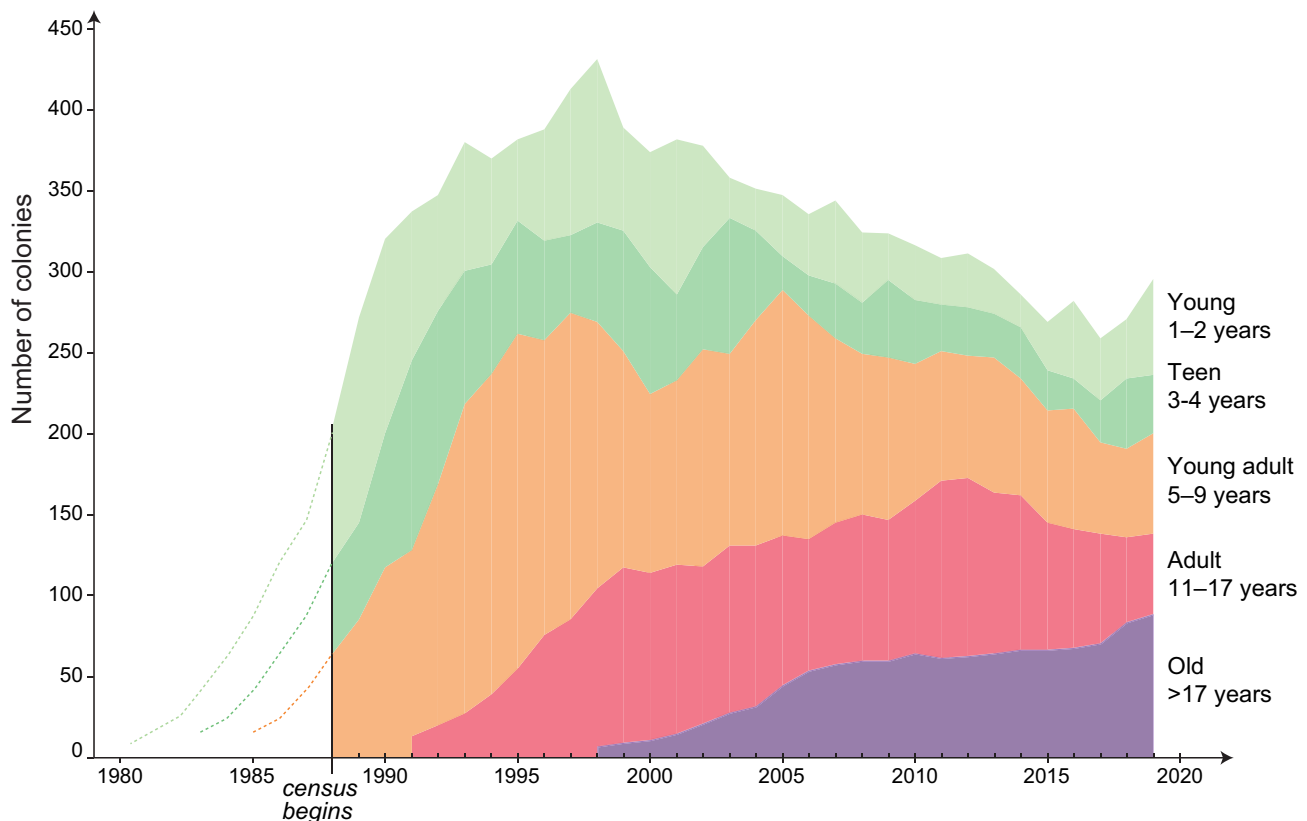


FIGURE 4 Change in population age structure over time. Each color shows the number of colonies of the indicated age. Dotted lines before 1988 show extrapolated ages; when the census began in 1988, all colonies with nest mounds as large as those of colonies known to be five were considered to be 5 years 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

which are likely to be more abundant when rainfall is high (Figure 3). Second, foraging activity is associated with humidity. Foragers lose water to evaporation when outside the nest. The permeability of ant cuticles to water is somewhat higher than for other xeric arthropods; and for the rough harvester ant *Pogonomyrmex rugosus*, water loss across the cuticle represents about 98% of total water loss while metabolic water loss is negligible (Lighton & Feener, 1989). When rainfall is high, the air is more humid, so water loss to foragers is lower (Friedman et al., 2019), and this makes foraging activity more feasible (Gordon, Dektar, et al., 2013).

Foraging activity and humidity

On the day-to-day and hour-to-hour timescales, foraging activity is closely associated with humidity (Pagliara et al., 2018). Ants lose water to evaporation while outside the nest searching for seeds. Some colonies are more likely than others to regulate foraging behavior so as to conserve water (Gordon, 2013; Gordon et al., 2011), by reducing foraging behavior on especially dry days. It appears that natural selection is shaping the collective regulation of foraging activity in response to humidity. During a period of drought, colonies that regulated foraging so as to conserve water were more likely to produce offspring colonies (Gordon, 2013). Differences among colonies in sensitivity to water loss are reflected in their foraging behavior (Friedman et al., 2019) and in the expression of genes associated with biogenic amines that appear to influence foraging activity (Friedman et al., 2020).

Food availability and rainfall

Colonies compete with their conspecific neighbors for foraging area in which to search for seeds. Food availability, in the production of seeds mostly by desert annuals, is associated with rainfall. Since seeds can travel by wind from the surrounding area, food availability may depend on rainfall in a wider region than the site. It has not been possible to examine food availability directly on the scale of the 10-ha site, except by tracking the food brought in by foragers (Gordon, 1993).

There is indirect evidence that food availability decreases when rainfall is low. An examination of 5 years of data from 1997 to 2002 showed that colony mortality was higher in times of low summer rainfall (Sanders & Gordon, 2004). The production of alate reproductives was lower in more crowded neighborhoods of colonies in 1995, after a year of low rainfall, than in 1997, after a year

of higher rainfall (Gordon & Wagner, 1997; Wagner & Gordon, 1999).

Interactions of neighboring colonies

Red harvester ant colonies normally forage for scattered seeds, so the discovery of a seed in one location does not warrant bringing other foragers to the same location. This species does not normally use trail pheromone to set up a trail to a food source, although they can form trails when researchers provide a pile of seeds early in the morning when the patrollers are active (Gordon, 1983). Each day a colony chooses among 4–8 habitual trails or fan-shaped streams of dispersed foragers, which extend up to 15–20 m from the nest (Gordon, 1991, 1995). Each forager leaves the nest, travels along in a stream of ants, and then leaves that stream or trail to search for seeds. The choice of foraging directions each day is mediated by the patrollers (Greene & Gordon, 2007), who come out early and meet the neighbors of neighboring colonies, then lay a chemical trail about 0.5 m long on the nest mound toward one of the habitual exits from the mound in a particular direction (Figure 3).

Colonies interact when the paths of the foragers of neighboring colonies intersect, leading the foragers of the two colonies to search in the same area. At least one foraging trail meets one of a conspecific neighbor's about once a day (Gordon & Kulig, 1996). Foragers can distinguish the odor of workers from neighboring colonies from those of more distant ones (Gordon, 1989), apparently as a result of frequent encounters between foragers (Esponda & Gordon, 2015; Sturgis & Gordon, 2013). Though brief encounters between neighbors are common, fighting is rare, occurring mostly on very humid days after the summer rains (Gordon & Kulig, 1996; Sturgis & Gordon, 2013). Fights can go on for 30 minutes or more, as one ant latches onto the petiole of another and attempts, usually unsuccessfully, to bite it in two, and thus fighting poses a risk of desiccation for both participants.

Colony interactions with neighboring colonies shift with colony life history (Gordon, 1992a; Gordon & Kulig, 1996). Foraging area does not scale linearly with colony age (Adler & Gordon, 2003); the foraging trails of a 3–4 year old colony are about as long as those of a mature, older, and larger one, reaching up to 15–20 m from the nest. However, interactions of neighboring conspecific colonies change as the colony grows older and larger. In a previous study, colonies were enclosed around the mound in order to prevent foraging, and the foragers of neighboring colonies soon began to search in the former foraging area of the enclosed colony (Gordon, 1992a). How a

colony reacted once its foragers were released, and met the encroaching foragers of their neighbors, depended on its age. Foragers of very young colonies, 1–2 years old, were likely to retreat when they encountered the foragers of a neighboring colony. By contrast, the foragers of a 3–4 year old colony, during the period of rapid growth before it reaches its mature size and begins to reproduce (Figure 1), were likely to engage in repeated confrontations with the foragers of a neighboring colony. Once a colony reaches reproductive maturity at 5 years, it is likely to avoid trails that overlap those of a neighbor. It appears that interactions of the foragers of neighboring colonies are mediated by encounters among their respective patrollers, early in the morning before foraging begins, which may influence the patroller's choice of foraging directions (Greene & Gordon, 2007).

The changes in a colony's interactions with neighbors, as the colony grows older and larger, may be related to changes in the need for food to feed the larvae. Since workers live only a year, the foragers of an older colony are not older than those of a younger one. However, the ratio of larvae to adult workers changes during the life history of a colony. For example, a 3–4 year old colony has about 6000 ants but must produce about 8000 workers by the following year, and thus has a higher ratio of larvae to foragers than an older, larger colony that has 10,000 ants available to produce another 10,000 the following year (Figure 1).

METHODS

To learn how competition for food structures spatial distributions, we examined the effect of local neighborhoods of conspecific colonies on survival and recruitment, and how this depends on rainfall.

Survival

Individual colony survival

We first considered the factors that affect the probability that an established colony will survive to the next year, using logistic regressions and mixed-effects logistic regressions.

Year-to-year changes in survival by age class

To learn whether there were any synchronous changes across age categories in annual survival to the following

year, we identified breaks in time series of survival estimates using piecewise regressions.

Recruitment

Factors affecting recruitment

We asked how neighborhood and rainfall affect the probability that a founding colony survives to be 1 year old, using simulations of possible founding sites and generalized linear models.

Year-to-year changes in recruitment

To learn whether there were temporal fluctuations in recruitment, we used negative binomial regression to ask how neighborhood and precipitation influence the number of 1-year-old colonies each year.

Patterns in the spatial distribution

Clustering within years

To examine whether there was overdispersion of colonies from year to year, we calculated Ripley's K, a measure of clustering, at different distances among colonies.

Year-to-year changes in clustering

To ask whether the overall degree of dispersion of colonies changes from year to year, we used two metrics that reflect clustering, variance-to-mean ratios (VMR) and Morisita's index.

Variables

The variables used in statistical analyses and their acronyms are shown in Table 1.

Rainfall

Rainfall data were obtained from the Western Regional Climate Center (<https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?az7560>) in San Simon, Arizona, located in the same arroyo as the study site, about 35 miles away. Although rainfall can be very local from day to day, on the monthly scale conditions are similar in San Simon to conditions at

TABLE 1 Variables used in statistical analyses

Variables	Acronym	Definition
Age class	age	
Young	–	1–2 years old
Teen	–	3–4 years old
Mature	–	>5 years old
Young adult	–	5–10 years old
Adult	–	11–17 years old
Old	–	≥18 years old
Modified Voronoi area	modArea	Intersection of Voronoi area and 15 m buffer around the nest
Distance to nearest neighbor	dist	Distance to the nearest neighbor (m)
Survival	–	Survival = 1 in year t if the colony was also alive in year $t + 1$, survival = 0 in year t if the colony was recorded as dead in year $t + 1$
Recruitment	–	Recruitment = 1 if colony appeared as a new colony with age = 1 year, recruitment = 0 for simulated points reflecting locations of colonies that failed to establish as a 1 year old colony
Annual precipitation	annP	Total precipitation (mm) from September 1st of $t - 1$ to August 31st to t
Summer precipitation	sumP	Total precipitation (mm) from June 1st of $t - 1$ to September 30th to t
Annual precipitation from the previous year	annP(-1)	Total precipitation (mm) from September 1st of $t - 2$ to August 31st to $t - 1$
Summer precipitation from previous year	sumP(-1)	Total precipitation (mm) from June 1st of $t - 2$ to September 30th to $t - 1$
Proportion of neighbors that are young	PY	Proportion of neighbors of age 1–2 years
Proportion of neighbors that are teens	PT	Proportion of neighbors of age 3–4 years
Proportion of neighbors that are mature (adult)	PA	Proportion of neighbors of age ≥ 5 years
Number of colonies	NC	Number of colonies in current year t
Average neighbor age	ageNeigh	Average age of neighbors
Average neighbor area	areaNeigh	Average Voronoi area of neighbors
Voronoi area	area	Voronoi area
Number of neighbors	NN	Number of colonies that share an edge of Voronoi area with focal colony
Annual precipitation from previous 5 years	annP5	Total precipitation (mm) from September 1st of $t - 5$ to August 31st of t
Annual precipitation from previous 10 years	annP10	Total precipitation (mm) from September 1st of $t - 10$ to August 31st of t
Summer precipitation from previous 5 years	sumP5	Total precipitation (mm) from September 1st of $t - 5$ to August 31st of t
Summer precipitation from previous 5 years	sumP10	Total precipitation (mm) from September 1st of $t - 10$ to August 31st of t
Number of neighbors identified with modified Voronoi area polygons	NNmod	Number of neighbors identified using modified Voronoi area
Average age of neighbors identified with modified Voronoi area maps	ageNeighmod	Average age of all the neighbors identified using modified Voronoi area

the site. We calculated total rainfall for each month. Some months included missing daily values. For these, we estimated total monthly rainfall by replacing the missing daily values with ± 10 year daily averages for the month in question.

We defined summer precipitation in year t as the total precipitation in millimeters from 1 June to 30 September of that year, summer precipitation of the previous year as the same for 1 June to 30 September of the year $t - 1$, annual precipitation as the total rainfall in millimeters occurring from 1 September of the year $t - 1$ to 31 August of year t , annual precipitation of the previous year as the same for 1 September of the year $t - 2$ to 31 August of year $t - 1$. Each total is the sum of the total rainfall for each month included.

Census methods and colony age

Each colony is identified by a number, which is on a marker at its nest mound, and its location is recorded, thus generating maps such as the ones shown in Figure 5. Each year in July or August, we censused all colonies, by checking whether each colony that was alive the year before was still alive and recording any changes of location because of moving, and we identified and recorded the location of all new colonies. A nest mound can be a meter wide or more; measurements of colony location are made at the nest entrance, which is up to a few centimeters wide and usually around the center of the mound. Until 1991, measurements were made using a compass and tape measure. Beginning in 1991, all

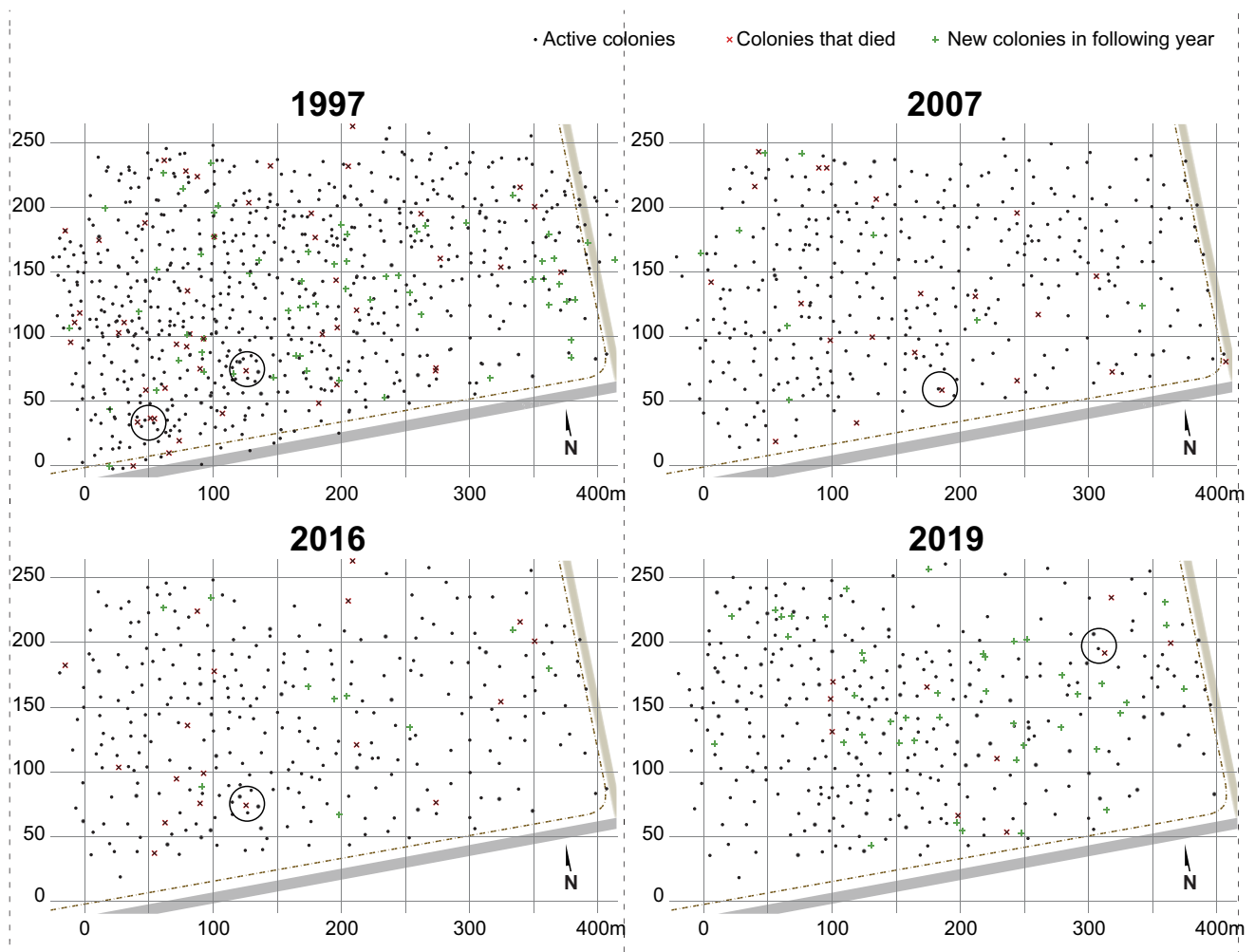


FIGURE 5 Maps of the colonies at the study site for 1997, 2007, 2016, and 2019. The gray stripe indicates a road along the southern edge of the site, and another road built in 2001 along the eastern edge. Maps are shown for 1997, when the number of colonies was high (see Figure 2); 2007, after numbers 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 \times 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 \times), and its neighbors (black dots)

measurements were made using a survey theodolite, and previous measurements were corrected.

Recorded ages of colonies ranged from 1 to 37 years. The age structure of the population has changed over the course of the study (Figure 4). Colonies reach a stable size when they reach reproductive maturity at about 5 years old (Gordon, 1992a) (Figure 1). In 1988, when the census began, all colonies that appeared large enough to be 5 years old, based on observations at the site made in the previous 7 years, were designated as 5 years old. However, these colonies could have been older than 5 years. Thus, the true age is known only for colonies that were new on the site, and designated as 1 year old, in 1988 or later. In the survival analyses in part I, we used only data from 2000, the 12th year of the study, and after, so as to eliminate colonies that could have been much older than their designated age.

For some analyses, we divided the colonies into age classes that correspond to changes in foraging behavior over the course of a colony's life history (Adler & Gordon, 2003; Gordon, 1992a, 1995; Gordon & Kulig, 1996). We considered the effects on recruitment of three age classes of neighbors: "young," ages 1–2 years, which have small foraging areas; "teens," quickly-growing colonies, ages 3–4 years, approaching reproductive maturity, which tend to be aggressive with neighbors; and "mature" colonies 5 years and older, which can send reproductives to the annual mating aggregation. We considered survival in three sub-classes of mature colonies older than 5: "young adult," 5–10 years old; "adult," 11–17 years old; and "old," 18 years or older.

Colonies sometimes move nests from one location to another (Gordon, 1992b). The proportion of colonies that move varies from year to year. For example, in some years of high rainfall when vegetation was very dense, colonies tended to move from areas of dense vegetation to more areas that are open. We have not found evidence that relocation by colonies affects nest distributions (Gordon, 1992b). The same colonies tend to move more than once, perhaps because of some form of pathogen that induces the colony to move but which the colony takes with it, eventually inducing another move. Since relocation takes many days and occurs during the monsoon season, which is when fieldwork has been done, many moves have been observed.

However, sometimes a move that has not been observed is suspected, because a large nest, apparently older than a newly founded colony, appears close to an abandoned one. Colonies tend to move along foraging trails (Gordon, 1992b), so a persistent foraging trail between the new nest and an older abandoned one suggests that the older colony has recently moved. Since 2010, we have been able to use the dependent-lineage haplotype (Gordon, Pilko, et al., 2013) to confirm the

identity of colonies suspected of moving, by comparing the haplotype of the new colony with records of the haplotype of the original colony. There remain 4.6% of the colonies (37 of 805 colonies considered when those at the edge were removed, or 49 of 1057 colonies considered in all) whose identity is not known because a move is suspected but not directly observed, and haplotype matching was not possible. To deal with this, we created two sets of data. In the first dataset, a colony was considered to move only if its move was confirmed by observation or by comparison of mitochondrial haplotype (Gordon, Pilko, et al., 2013). In the second dataset, a colony was considered to move if it appeared to match in age a nearby colony with a recently abandoned nest and had foraging trails that connected the new colony with the abandoned nest. We performed the analyses of individual colony survival ("Individual Colony Survival" section) and recruitment ("Factors Affecting Recruitment" section) with both data sets. The two data sets differed in 4.5% or 325 of 7298 colony-year observations.

Recruitment of new colonies

To examine the effects of the neighborhood of conspecific colonies on the survival of newly founded colonies, we considered how the neighborhood influences whether a founding colony could persist at a particular location from year 0, the year it is founded, until the next year when it is 1 year old.

A new colony is designated as 1 year old, founded by a queen that mated in the previous year's mating flight. The census has been conducted each year between late July and early September; the mating aggregation in which a 1-year-old colony's queen mated occurred in late July or early August of the previous year (Gordon & Wagner, 1997; Wagner & Gordon, 1999). The size of new colonies varies from year to year, and within a year, new colonies differ in size. Often new 1-year-old colonies have a nest entrance at the base of a plant or small bush, which then dies as the nest expands underneath its roots. New colonies are usually discovered by tracking the foragers back to the nest. In some years with heavy rainfall, dense vegetation may hide the small foraging trails of 1-year-old colonies, and those colonies are most likely to be found the following year when their foraging trails are more conspicuous.

When a new colony appears to have many more ants than the smallest new colonies of the same year, it is designated as 2 years old, and its location is designated retroactively as the same in the previous year, presuming that it was missed the previous year. This estimate is made each year by comparing the nests and foraging trails of the smallest new colonies of that year with the 2-year-old colonies that were the smallest 1-year-olds in the

previous year. A new colony is considered large enough to be designated as 2 years old based on two criteria for estimating colony size. First, on a day after rain, the new colony has a pile of excavated soil about twice the area than those of the smallest new colonies of that year; this indicates colony size assuming that larger colonies need more nest chambers than smaller ones, and have more ants to excavate and carry out more soil. Second, the new colony has more than about three times the number of foragers active than the smallest new colonies on the same day. Between 1988 and 2019, 593 colonies were found when 1 year old and 223 were found when 2 years old.

Survival

We defined survival as a binary variable, where 1 indicates survival of the colony to the next year and 0 indicates death of the colony in the next year. Thus, survival = 1 in year t if the colony was also alive in year $t + 1$, and survival = 0 in year t if the colony was recorded as dead in year $t + 1$.

Of the 1057 colonies identified from 1988 to 2020, 750 have died. In each year's census, a colony is considered to be active if we observe both returning foragers, carrying food into the nest, and ants leaving the nest, either to join a foraging trail to search for seeds, or to carry out refuse (Gordon, 1984). This makes it possible to distinguish a colony that is truly active at its own nest from one whose foragers are entering the abandoned nest of a dead neighboring colony to take what remains of the dead neighbor's stored seeds. When ants are taking seeds from an abandoned nest, ants are seen leaving the old nest with food and entering another one, but they do not take anything into the abandoned nest.

A colony is considered to be dead when it is consistently inactive, over many days, in two successive years. A colony does not forage every day, so inactivity on any given day does not mean the colony is dead. Colonies that are not active are checked 4–5 times in the course of a field season, especially on days after rain when most colonies are active. Since workers live for about a year (Gordon & Holldobler, 1987), a year can elapse between when the queen dies and when the last workers have died. During this time foraging activity declines, as there is less brood to feed, and the mound tends to become overgrown. Laboratory observations suggest that sometimes workers produce haploid males for the annual mating aggregation after the queen has died. As rainfall has declined over the course of the study, so has foraging activity, and so since about 2010, if a colony is not seen active 1 year, we check again the following year. Over the course of the study, 84 colonies were found active 1 year

after being inactive on all days checked in the previous year's field season.

Identifying conspecific neighbors using Voronoi tessellation

To identify the conspecific neighbors of each *P. barbatus* colony, we used Voronoi tessellations to generate a polygon around the location of each colony's nest (Figure 6), using a tessellation method based on Delauney triangulation (using R package “deldir”; Turner, 2002). This method has been used to examine the interactions of neighboring ant colonies (Adams, 2001) and more generally, neighbor interactions in vegetation and in sessile animals (Pringle & Tarnita, 2017).

For our analyses of the effects of neighbors on colony survival and recruitment, we identified as neighbors only the colonies adjacent in the tessellation, sharing an edge. The foraging area of a colony is bounded by the foraging areas of neighboring colonies. Trails extend radially from each nest. Foragers do not proceed past a place where they meet foragers of another colony, so the trail of one colony never crosses the trail of a neighbor (Gordon & Kulig, 1996). The Voronoi tessellation defines the line between a pair of neighboring colonies, where the foragers heading out from one colony would block the trail of the neighbor (Figure 6). Thus, the edges of the Voronoi polygon identify the neighbors whose trails those of the focal colony are likely to meet, and excludes nearby colonies that are located behind others so that their trails are not likely to penetrate the barrier created by the trails of the functional neighbors.

Colonies on the boundary of the study site

To eliminate edge effects, the colonies on the boundary of the site, and all of their Voronoi neighbors, were removed from the analyses. A colony was considered to be on the boundary if it has no neighbor on the site on at least one edge of its Voronoi polygon, and the neighbors of the boundary colony were all the Voronoi neighbors, that is, all colonies that shared an edge with it. We determined which colonies were on the boundary or were neighbors of the boundary colonies with the Lewis Aboav-Weiare algorithm, using the “lawSummary” function from R package “deldir” (Turner, 2002).

Measuring foraging area using Voronoi tessellations

To derive a measure of a colony's foraging area, and thus the extent of crowding by its neighbors, we used a

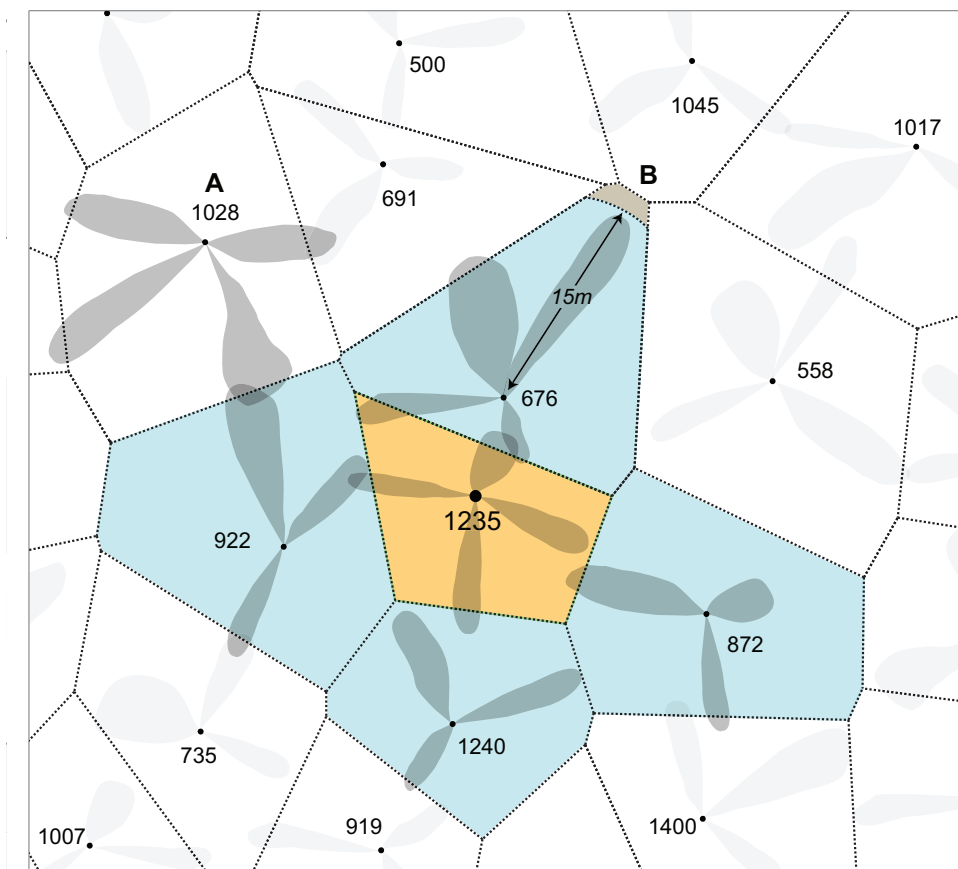


FIGURE 6 Illustration of Voronoi tessellation to identify neighbors and estimate foraging area. Black dots show the locations of the nests of the indicated colonies. Dotted lines show the outlines of Voronoi areas. The shaded gray shapes illustrate hypothetical foraging trails, taken from maps of foraging 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

modified version of the area of the polygon defined by the Voronoi tessellation (Figure 6). A colony’s foraging area tends to have more convex edges than a polygon formed by straight lines (Gordon, 1995). Foraging trails can extend up to about 20 m, but are usually shorter, especially in young colonies, 1–2 years old (Adler & Gordon, 2003; Gordon, 1995). Some Voronoi polygons in the tessellation had protruding shapes that extended more than 20 m from the nest, which is further than foragers are likely to travel. To eliminate this extra foraging area generated by the shape of the Voronoi polygon, we measured foraging area as the area of the intersection of the Voronoi polygon with a circular buffer of radius 15 m. The buffer was computed with “gBuffer” and the geometric intersection with “gIntersection” in R package “rgeos” (Bivand & Rundel, 2012). The foraging area, the

area of the modified Voronoi polygon, was estimated using “gArea” (Bivand & Rundel, 2012).

Distance to nearest neighbor

To evaluate how the proximity of neighbors affects the survival of newly founded colonies, we considered the distance to the nearest conspecific neighbor. This measure does not capture the effects of the neighbors on all sides that may encroach on the foraging area of a focal colony. However, observation suggests that distance to the nearest neighbor is crucial for newly founded colonies, because a new nest that is very close to an older, large neighbor is likely to be overrun by the foragers of the older neighbor, which deters the foragers of the new

colony from leaving the nest. To find the nearest neighbor, we calculated pairwise Euclidean distances between the focal new colony and all other colonies in the study area alive in that year. The distance to the nearest neighbor was the minimum distance among all pairwise distances.

Data analysis

Survival

Individual colony survival

We first considered the factors that influence the probability that an established colony survives to the next year. We performed logistic regressions with 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 proportion 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 (Table 1). We found significant high correlation coefficients among Voronoi area, modified Voronoi area, average modified Voronoi area of all Voronoi neighbors, and distance to nearest neighbor (Appendix S1: Table S1). We then performed regressions with only modified Voronoi area as a predictor, omitting the other measures associated with the foraging area, as this measure most directly captures the foraging area available to a colony. The proportion of neighbors that are young and the proportion of neighbors in the other age classes, teen and

mature, are significantly correlated because these proportions are not independent of one another. We used the proportion of neighbors that are young as a predictor. The remaining variables were also tested. To test for a lagged effect of rainfall on survival, we also predicted survival with precipitation from the previous 5- and 10-years periods, using a generalized linear model. These analyses (in “Individual Colony Survival”) considered 7298 colony-year observations for 805 colonies, after those on the edge of the study site and their neighbors were removed.

We defined a set of nested candidate models (Table 2) and added independent predictors sequentially. The best model was selected using likelihood ratio tests, Aikake Information Criterion (AIC) values, and proportion of survival observations correctly predicted by models. We computed the proportion of observations predicted correctly using the leave-one-out (LOO) cross-validation method (Ugarte et al., 2016), which involves dropping each row of data sequentially, fitting a generalized linear model (or generalized linear mixed-effects model) to the remaining data, and predicting the survival of the observation that was dropped from computed coefficients and predictors. The number of correctly predicted observations was tallied for the final model.

To account for non-independence and potential random year and colony effects, we also constructed generalized linear mixed-effects models using the R package “lme4”. As in the generalized linear models, we predicted survival with fixed effects for modified Voronoi area, proportion of neighbors that were young (1–2 years), summer precipitation, summer precipitation from the previous year, annual precipitation, annual precipitation from the previous year, and random intercepts for year and colony ID. All predictive variables for mixed-effects

TABLE 2 Likelihood ratio tests of nested candidate models explaining colony survival

Models	AIC	BIC	Residual df	LRT	p-Value	Loo R ²
I + (1 YEAR)	3721.8	3735.6	7296			0.63
I + (1 YEAR) + age	3688.6	3729.9	7292	41.218	<0.001	0.689
I + (1 YEAR) + age + modArea	3640.5	3688.7	7291	50.122	<0.001	0.717
I + (1 YEAR) + age + modArea + sumP(−1)	3642.2	3697.4	7290	0.263	0.608	0.717
I + (1 YEAR) + age + modArea + sumP(−1) + annP	3643.3	3705.4	7289	0.883	0.347	0.713
I + (1 YEAR) + age + modArea + sumP(−1) + annP + PY	3643.7	3712.6	7288	1.64	0.2	0.702
age + modArea	3671.3	3712.694	7292	–	–	0.68
age + area	3679.2	3720.566	7292	–	–	0.68

Note: For each model tested, the table provides AIC values, residual degrees of freedom (residual df), likelihood ratio test statistic (LRT), and accompanying p-value testing significance of each model and the previous model. Model variables are “age”, age class (“young” 1–2 years, “teen” 3–4 years, “young adult” 5–10 years, “adult” 11–17 years, “old” >18 years); “modArea” modified Voronoi area in square meters, “area” is Voronoi area in square meters, “sumP,” summer precipitation from current year (in mm); “annP,” annual precipitation (in mm), “PY,” proportion of neighbors that are young, “PA,” proportion of neighbors that are mature (adult). Variables are defined in Table 1. The intercept or null model is represented as “I” and random intercept for year as “1|YEAR.” Abbreviation: BIC, bayesian information criterion.

models were standardized by subtracting the mean and dividing by the standard deviation.

Because the results of this analysis showed that foraging area is associated with survival, we further tested whether foraging area, and the range among colonies in foraging area, change from year to year. We performed linear regression analyses predicting the logarithm of modified foraging area with year, and, separately, the logarithm of the range of modified foraging areas, calculated as the difference between the largest and smallest modified foraging areas of any colonies in that year.

Year-to-year changes in survival by age class

To learn whether there were any synchronous changes across age classes in annual survival to the next year, we identified breaks in a time series of survival estimates between 2000 and 2019. We did not look for break points prior to 2000, as results could have been influenced by underestimating the ages of colonies assigned the age of five when the census began in 1988. We first identified significant break points in annual survival estimates, and then tested whether the same break point was significant for each age class. For the annual survival of all colonies, we determined the break point using an iterative procedure and a piecewise regression method (Crawley, 2012). This method predicts annual survival as a function of the year in a linear model with additional slope estimates and accompanying *t*-statistics and *p*-values, to explain changes in survival before and after the break point. The most significant break was the year in which survival or slope changed statistically before and after the estimated break point. Once we determined which year produced the largest change in annual survival, we tested which age class (young, teen, young adult, adult, and old) contributed to this change. For every age class, we calculated annual survival to the next year, fit the piecewise regression at the estimated break point, and then tested for significant changes in survival by evaluating the *t*-statistics and *p*-values for the slope at the break point.

Because this analysis indicated that there was a break point in the survival of colonies in the 'adult' and 'old' age classes, ≥ 11 years old, we compared the foraging areas of colonies of this age class that did and did not survive to the following year. We performed a bootstrap analysis to compare the modified foraging areas of colonies that survived and died for each year between 2011 and 2019. For each year, we calculated the 95% bootstrap confidence intervals from 999 samples for logarithm-transformed modified foraging areas of colonies that survived and compared this to the mean modified foraging area of colonies that died.

Recruitment

Factors affecting recruitment

To learn how neighborhood and rainfall affect the probability that a founding colony survives to be 1 year old, we used generalized linear models. We asked which colonies founded after the mating aggregations in 1 year survive to be 1 year old the following year. For each year, we compared the observed distribution of new 1-year-old colonies to a simulated distribution of colonies founded by newly mated queens in the previous year, year 0. We simulated the distribution of the nests of newly mated queens in year 0 using a random Poisson process, implemented by "spatstat" (Baddeley & Turner, 2005), to distribute background points across the study area at a density of 0.0002. This density is equivalent to ~ 1000 background points distributed evenly across the study area, corresponding to estimates from counts of numbers of reproductives leaving for the mating flight (Gordon & Wagner, 1997; Wagner & Gordon, 1999). Since a founding queen that lands on the mound of another colony would be killed by that colony's workers right away (D.M. Gordon, personal observation), we removed from the simulation all points representing nests made by newly mated queens in year 0 within 2 m of an established nest. Recruitment was defined as a binary variable; 1 represents the successful establishment of a 1-year-old colony, and 0 represents a simulated colony that did not survive to be 1 year old.

For each year, we constructed a Voronoi map of all established colonies and simulated nests made by newly mated queens, and used this to identify the neighbors of each colony. We then extracted predictors for all 1-year-old nests, including distance to the nearest neighbor, the average age of neighbors, and the proportion of neighbors that are mature, >5 years old. The proportions of neighbors that were young and teens were highly correlated with the proportion that were mature, and both were removed from regressions. We did not choose the proportion of neighbors that are young, as in the survival analysis, because the young neighbors included the simulated locations of possible new colonies. As in the survival analyses, we removed all colonies at the edge of the study site and their neighbors. The final dataset included all the colonies that survived to be 1 year old in the current year, and the simulated new nests from year 0, the previous year, that did not survive to the current year.

We performed a logistic regression predicting recruitment as a function of distance to the nearest neighbor, the proportion of neighbors that are mature (>5 years), the average age of neighbors, summer precipitation of the current year when the colony is 1, summer precipitation from the previous year when the colony was founded,

annual precipitation the year the colony is 1 year old, and annual precipitation from the previous year when the colony was founded.

To ensure that regression results were robust to the randomization process, we repeated the random Poisson process and created 500 different simulated background datasets. For every run, we created a Voronoi map of simulated new nest sites and colony locations from the year the colony is 1 year old. The R package “bestglm” was used to automate the selection of significant predictors through a search algorithm and the “leaps” procedure with an AIC criterion and to find the best logistic regression model for each dataset. The bestglm package uses a simple exhaustive search algorithm (Morgan & Tatar, 1972) and the leaps branch-and-bound algorithm (Lumley & Miller, 2004) to choose models with minimal deviance (McLeod & Xu, 2010). Because these procedures can overstate the significance of predictors (McLeod & Xu, 2010), we bootstrapped results across 500 different simulated background datasets. For all 500 runs, we saved the final best model and the accompanying slopes of standardized predictor variables. From the histogram of predictor variables and slopes, we found the proportion of times each predictor variable was selected as a significant predictor of recruitment, and then summarized the coefficients of the predictor variables and their accompanying z-statistics.

Year-to-year changes in recruitment

To learn whether there were temporal fluctuations in recruitment, we asked how neighborhood crowding variables and precipitation influence the number of 1-year-old colonies in a given year. To do this, we performed a series of negative binomial regressions. Using “glm.nb” in library MASS, we modeled the annual number of new 1-year-old colonies as a function of the average modified Voronoi area of all colonies from the previous year when those colonies were founded, the average distance to the nearest neighbor of all colonies in the previous year when those colonies were founded, the total number of colonies on the site in the previous year when those colonies were founded, summer precipitation of the same year when those colonies were 1 year old, and annual precipitation from the previous year from founding to when those colonies were 1 year old. The best model was identified using likelihood ratio tests.

Patterns in the spatial distribution

We asked whether changes in the effect of neighbors on survival, over the course of the study, could have been related to changes in the clustering pattern of the

colonies. We considered whether crowding due to clustering could account for the result that survival of “young adult” colonies tended to decrease after about 2001–2003, when precipitation and recruitment of new colonies began to decline (Figure 2).

Clustering within years

First, to examine the spatial distribution of colonies each year, we calculated Ripley’s K (Dale & Fortin, 2014), a measure of clustering, at different distances among colonies, and considered how these spatial patterns changed over time.

Ripley’s K measures the degree of clustering or overdispersion of points at different distances to examine spatial distributions at different scales. We tested for changes in clustering and overdispersion by estimating Ripley’s K in years 1997, 2007, 2016, 2019, using the R package “spatstat” (Baddeley & Turner, 2005). We chose these years to include a year at the beginning of the peak in colony numbers in about 1997–1999 (1997); a year after the drought began in about 2001–2003 (2007); the year when the results of the survival analysis showed a decline in colony survival (2016); and the most recent year for which complete data were available (2019) (Figure 2).

We compared the value of Ripley’s K to the value representing the null hypothesis that points were distributed under complete spatial randomness, in 100 iterations using the functions “envelope” and “Kest” (Baddeley & Turner, 2005). Departures of the observed Ripley’s K function from null envelopes suggest significant clustering if $K > \text{envelope}$, or significant dispersion if $K < \text{envelope}$ (Baddeley, 2010; Boulay et al., 2010). Because we found significant departures from complete spatial randomness, indicating a non-random distribution of colonies, we tested different models of point distribution including a Poisson point process, Strauss point process, and non-stationary variants of Poisson and Strauss point processes (Baddeley, 2010). We compared simulations from each point process to the observed value of Ripley’s K using the function “envelope.” The final model had the lowest AIC value and had a confidence envelope from 100 iterations that overlapped the observed colony clustering patterns as described by Ripley’s K function over distance (Baddeley, 2010).

Year-to-year changes in clustering

To investigate the changes from year to year in the degree of clustering, we used two metrics: VMR and Morisita’s index (Dale & Fortin, 2014; Krebs, 1999). We calculated both metrics using both distance and quadrat-based measures. Because the distance-based measures, such as the Clark–Evans metric, corrected for boundary effects using

the Donnelly correction (Krebs, 1999), generated results similar to those from quadrat-based measures, here we report only the results of the quadrat-based metrics.

We divided the study area into quadrats using “quadratcount” in R and calculated VMR (Krebs, 1999). When the variance in the number of colonies per quadrat is larger than the mean (VMR > 1), nests are clumped; if the variance is equal to the mean (VMR = 1), nests are distributed randomly; and if the variance is lower than the mean (VMR < 1), nests are dispersed. We calculated VMR for a range of quadrat sizes from 15 m × 15 m to 137 m × 137 m and plotted VMR by year.

We used the Morisita’s index as a second measure of crowding. A Morisita’s index value >1 indicates clustering, a value of 1 indicates a random pattern, and a value <1 suggests dispersion. Because the value of this measure is sensitive to quadrat size (Krebs, 1999), we calculated the Morisita’s index at different quadrat sizes and plotted the spatial scale at which clustering was observed. For each year, we identified the quadrat size at which the Morisita’s index was highest and >1, indicating clustering, using the function “mipLOT” in the R package “spatstat.” We then considered whether there was clustering at any spatial scale that persisted over time.

RESULTS

Survival

Individual colony survival

The probability that a colony survives to the next year depends on its age and on the size of its foraging area. The younger the colony, the more likely it is to survive. The larger its foraging area, the more likely it is to survive.

The best predictors of survival were colony age and the modified Voronoi area. These predictors were identified by likelihood ratio tests, the proportion of observations correctly predicted, and AIC values (Table 2). Both age and modified Voronoi area were consistently identified as important variables, even after accounting for random year effects in mixed-effects models (Table 2). The probability of survival was highest for young colonies and lowest for old colonies (Table 3 and Figure 7). Survival was high for colonies with large foraging areas, relative to colonies with smaller ones (Table 3, Figure 9 and Appendix S1: Tables S2, S3). The probability of survival did not depend on precipitation or the proportion of neighbors that were young (Table 2).

The extent to which colony age and foraging area each predicted survival changed over the course of the

study. In the first part of the study until about 1997–1999, colony age predicted survival better than foraging area, while after the decline in rainfall that began in 2001–2003, and especially after 2005 (Figure 8), foraging area was a better predictor of survival (Table 3, Figures 8 and 9). The regression coefficient for the modified foraging area is positive, showing that a larger foraging area is associated with higher survival (Table 3). Colonies with large foraging areas were generally more likely to survive, but the effect of foraging area was much stronger after about 2001–2003. Both modified foraging area and the range of foraging area changed over time (regression results; Appendix S1: Table S2). The mean foraging area was lower, and the range of foraging areas was larger, in earlier years when colony numbers and precipitation

TABLE 3 Summary of the best mixed-effects logistic regression model, identified using likelihood ratio tests and AIC values

	Estimate	SE	z-value	p-Value
(Intercept)-Teen	2.935	0.147	19.935	<0.001
Young	0.806	0.194	4.161	<0.011
Young adult	0.017	0.139	0.120	0.904
Adult	−0.232	0.150	−1.551	0.121
Old	−0.569	0.179	−3.173	0.002
modArea	0.534	0.079	6.747	<0.001

Note: The table shows the coefficient estimate, standard error, z-value, and p-value for each variable. Model variables are age class (“young” 1–2 years, “teen” 3–4 years, “young adult” 5–10 years, “adult” 11–17 years, “old” 18 years or more) and “modArea,” average modified Voronoi area.

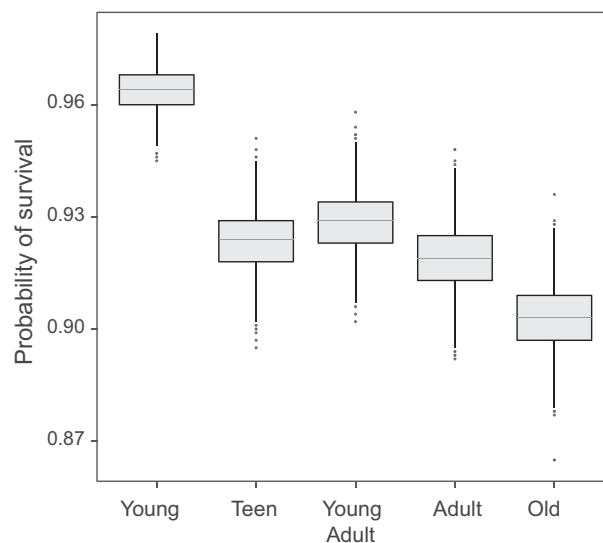


FIGURE 7 Probability of survival to the following year by colony age class. Young, 1–2 years; Teen, 3–4 years, Young adult, 5–10 years, Adult, 11–17 years; Old, >18 years

were high (Figure 10a). Colonies older than 11 years with small foraging areas (measured as modified Voronoi area) were likely to die in the later years of the study (Figure 10b). The 95% confidence intervals of foraging areas of colonies older than 11 years that survived were significantly larger than the mean foraging areas of colonies that died in 2011, 2012, 2013, 2017, and 2018 (bootstrap test, Appendix S1: Table S3).

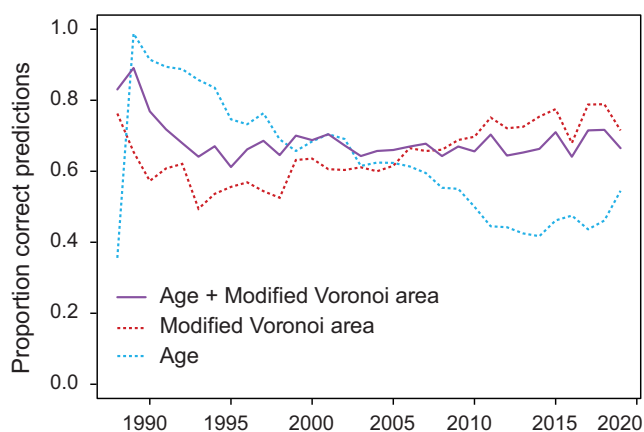


FIGURE 8 Proportion of correct predictions made by best predictors. Each line shows the change over time of correct predictions made by generalized linear models predicting colony survival using the indicated variables: purple, colony age, and modified Voronoi area; red dotted line, modified Voronoi area blue dotted line, colony age

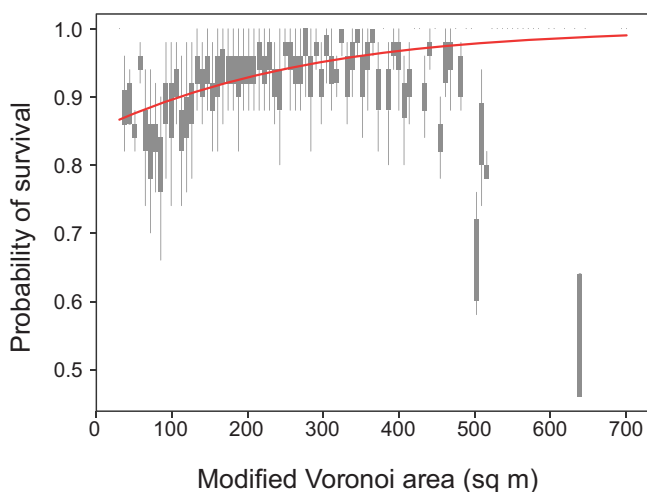


FIGURE 9 Probability that a colony survives to the following year as predicted by foraging area, which is measured by modified Voronoi area (m^2). The red line represents predictions from a generalized linear model predicting colony survival for a range of modified Voronoi areas. The boxplots represent the observed probability of survival across 50 bootstrap replicates for each bin of modified Voronoi area

We calculated the effects on survival of two estimates of foraging area: Voronoi area and modified Voronoi area. The modified Voronoi area excluded regions of the Voronoi polygon that were more than 20 m away and thus were unlikely to be used by foragers. The results for both were similar, but the AIC value with modified Voronoi area (AIC = 3671) was lower than the value for Voronoi area (AIC = 3679), suggesting that the modified foraging area was a better predictor of survival than the Voronoi area (Table 2). The regression results were also similar for the two data sets that differed in the IDs assigned to the 4% of colonies that may have moved, the one in which a colony that might have moved was given a new ID, and the one that used hypothesized IDs for those colonies (see Appendix S1: Table S4). The best

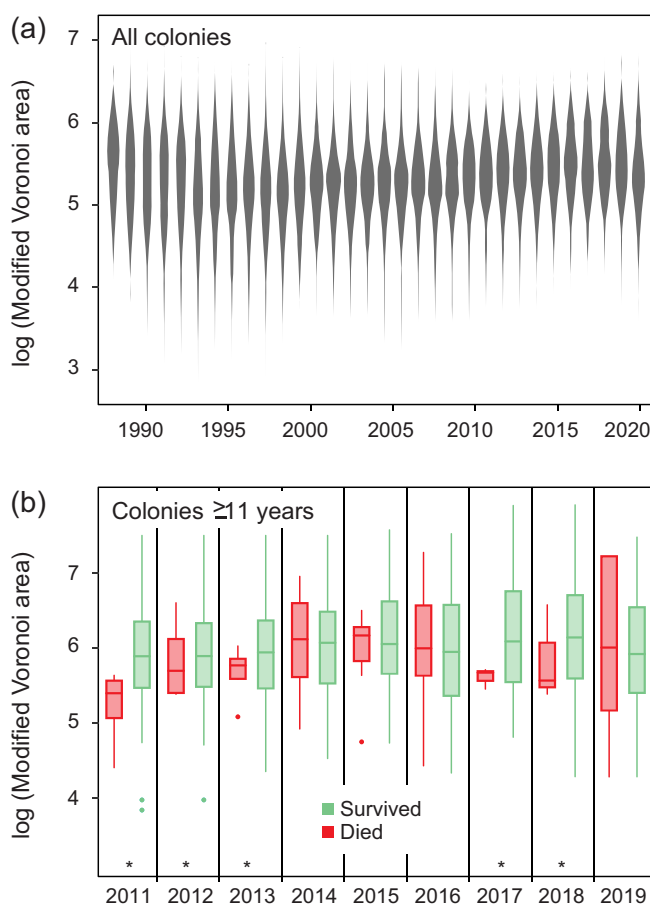


FIGURE 10 Changes in foraging area over time. (a) Violin plot of log-transformed modified Voronoi area of all colonies from 1988 to 2019. The height of the shape represents the range, and the width represents the density of points at that value of foraging area. (b) Relation of survival and log-transformed modified Voronoi area of long-lived colonies (age ≥ 11 years) from 2010 to 2016. Red indicates the foraging areas of colonies that died the following year, and green shows the foraging areas of colonies that survived until the following year. * indicates significantly larger foraging areas of colonies that survived (bootstrap analysis, Appendix S1: Table S3)

logistic regression model with age and modified Voronoi area correctly predicted 68% of observations of whether a colony survived to the next year, using the LOO method and without any random effects.

Both foraging area, estimated as modified Voronoi area, and colony age were significant factors explaining survival, even after accounting for non-independence due to random year effects. The final model included fixed effects for modified Voronoi area and age class, as well as a random intercept for year, and correctly predicted 72% of observations of whether a colony survived to the next year (Table 2). Other factors, including annual precipitation and proportion of neighbors that are young, did not improve the percent of observations of colony survival correctly predicted or fit using likelihood ratio tests (Table 2).

We found no effect of lagged precipitation variables for the previous 5 or 10 years on colony survival (Appendix S1: Table S4).

Year-to-year changes in survival by age class

The influence of colony age on survival changed over the course of the study. As rainfall declined, colonies were more likely to die when they were young adults, ages 5–10 years, rather than surviving into their 20’s. Using a piecewise regression and an iterative search method of all break points from 2000 to 2019, we determined that overall, annual survival decreased in 2016. This break point in survival rate in 2016 was primarily due to the significant drop in survival in 2016 for “young adult” colonies of ages 5–10 years (Figure 11; Appendix S1: Table S5 shows intercepts and coefficients for years before 2016 for each age class from piecewise regressions). The foraging areas of colonies that survived to the next year, however, were not larger than those of colonies that died in 2016 (Figure 10b). These break point results thus indicate that there are further factors that influence colony survival, in addition to competition with neighbors for foraging area.

Recruitment

Factors affecting recruitment

A newly founded colony was likely to survive to be 1 year old if precipitation was high, both in the summer of the previous year, when it was founded, and in the current year since it was founded (Table 4). A newly founded colony was also more likely to survive if its distance to its nearest neighbor was high (Table 4). The remaining variables did not show any significant effect on recruitment

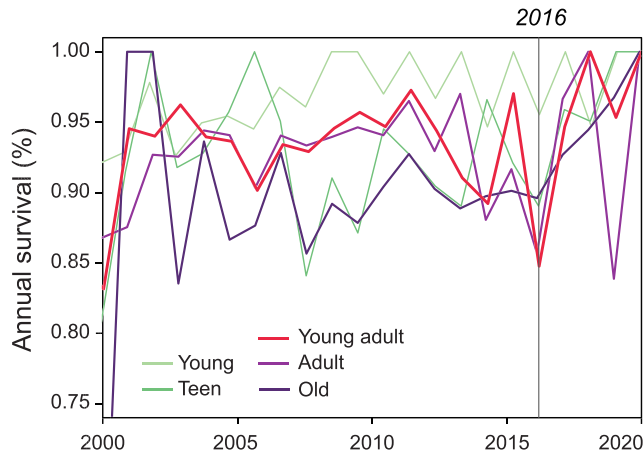


FIGURE 11 Annual survival rates, in proportion of colonies that survived to the following year, by age class. Young, 1–2 years; Teen, 3–4 years, Young adult, 5–10 years, Adult, 11–17 years; Old, 18 years and older. The significant dip in annual survival in 2016 was estimated from piecewise regressions

when summarized across 500 simulations, or were not selected consistently as a significant predictor of recruitment (proportion of runs <0.75; Table 4). Results were similar for the two data sets that differed in the assignment of colony ID to colonies suspected of moving (compare Table 4 with Appendix S1: Table S6).

Year-to-year changes in recruitment

The number of new colonies founded annually was best predicted by annual precipitation in the year since the colony was founded (Figure 2). Likelihood ratio tests of all other predictors were not significant, and AIC values of all other models were high (see Appendix S1: Table S7 for a list of all models tested). The number of new colonies was positively related to annual precipitation (Table 5).

Patterns in the spatial distribution

Clustering within years

For all years tested (1997, 2007, 2016, 2019), there was significant overdispersion of nests at small spatial scales under about 8–10 m, and clustering at larger scales over about 12–16 m. Ripley’s K reveals distributions that differ from a completely random process (Figure 12). In the panels on the left in Figure 12, the black line representing Ripley’s K dips below the gray envelope representing random distributions at distances below about 8–10 m, indicating overdispersion at small spatial

TABLE 4 Summary of logistic regressions predicting successful recruitment relative to background points

Variables	Proportion $n = 500$ runs	Lower confidence bound	Median	Upper confidence bound
sumP	0.018	1.421	1.472	1.647
sumP(-1)	1.000	4.788	5.522	6.158
annP	1.000	4.255	5.246	6.151
annP(-1)	0.056	1.423	1.507	1.886
ageNeigh	0.506	-2.815	-2.139	-1.466
dist	1.000	3.672	4.944	6.186
PA	0.290	1.438	1.940	2.567

Note: Columns show for the most important variables explaining successful recruitment: Proportion of times a variable significantly predicts recruitment in $n = 500$ runs; lower, median and upper confidence bound of the accompanying slope t -statistics. Positive values in slope t -statistics indicate a positive relationship with recruitment; negative values indicate an inverse relationship with recruitment. "sumP," summer precipitation of current year (in mm); "sumP(-1)," summer precipitation of previous year; "annP," annual precipitation of current year (in mm); "annP(-1)," annual precipitation of previous year (in mm); "ageNeigh," average age of neighbors; "dist," distance to nearest neighbor; "PA," proportion of neighbors that are mature (adult), >5 years old.

TABLE 5 Best negative binomial regression model to predict the annual number of new 1-year-old colonies (intercept, slope estimate, standard errors, z -value, and p -values)

	Estimate	SE	z -value	Pr ($> z $)
Intercept	2.464	0.342	7.208	<0.001
annP	0.077	0.031	2.470	0.014

Note: The best model, including only annual precipitation "annP" as a predictor, was identified using likelihood ratio tests summarized in Appendix S1: Table S7.

distances between nests less than 8–10 m. At larger distances, there is clustering above about 12–16 m; the black line representing Ripley's K is above the gray envelope representing random distributions.

The best model to explain spatial distributions was a non-stationary (second order polynomial for latitude and longitude) Strauss point pattern at $r = 8$ m. We tested this for 2019 and found that this model had the lowest AIC value when compared to other models (see Appendix S1: Table S8). Figure 12 shows that for all 4 years examined, the observed distributions generally fit the non-stationary Strauss point pattern. The Strauss point pattern at r of 8 m leads to overdispersion; the black line is generally contained within the gray envelope. The second order polynomial function fit to latitude and longitude shows clustering at larger spatial scales; the black line is within the gray envelope all the way up to 20 m.

In summary, there is significant overdispersion at small spatial scales of about 8–10 m, because K is lower than the null model of complete spatial randomness. The results also indicate clustering at larger scales above about 12–16 m, because K is higher than the null model of complete spatial randomness (Figure 12).

Year-to-year changes in clustering

The within-year analyses of changes in clustering do not show any spatial effects that account for the decreased survival of young adult colonies, ages 5–10, in the later part of the study around the break point of 2016 (Figures 11 and 13). We considered the possibility that although the total number of colonies at the site had declined (Figure 2), the lower survival of young adult colonies in the later part of the study was due to locally crowded neighborhoods, but this is not what we found. There were no obvious changes in clustering as precipitation and annual recruitment have declined (Figure 2).

Colonies tended to be more dispersed after 1997–1999, the years when colony numbers were highest. Both the VMR and Morisita's index analyses show more dispersion in later years at the same spatial scale (Figure 13). The variance-to-mean ratios (VMR) decline over time for all quadrat sizes, indicating that there is more clustering ($VMR > 1$) in the earlier part of the study, and it decreased as the number of colonies decreased after about 1997–1999 (Figure 13a). The Morisita's index analysis did not reveal any consistent pattern of clustering that persisted over time (Figure 13b). Clustering occurred on smaller spatial scales from about 1992–1998, when the number of colonies at the site was highest, but otherwise fluctuated across spatial scales from about 40 to 80 m² until reaching a large scale of about 120 m² after 2014 (Figures 5 and 13b).

The Ripley's K analysis for different years also suggests that crowding did not increase over the course of the study; there was no apparent reduction in overdispersion comparing 1997, the earliest year tested, with

the later years tested. Instead, the significant overdispersion in 1997 at spatial scales below 8–10 m persisted in years 2007, 2016, and 2019 (Figure 12).

DISCUSSION

Both colony survival and the recruitment of new colonies were influenced by the partitioning of foraging areas in local neighborhoods of colonies. Changes in rainfall influence the role of colony life history in competition with neighbors. In the earlier years of the study, when rainfall was high, colony numbers increased, and then began to decline after about 1997–1999, apparently due to crowding. As rainfall decreased, beginning in about 2001–2003, recruitment declined, and so did colony survival, leading to a trend toward earlier colony death, which was most pronounced in 2016.

Colony survival

Whether a red harvester ant colony survives from 1 year to the next depends on its age. The younger the colony, the more likely it is to survive, and most colonies live for more than 20 years. A colony’s survival also depends on the spatial distribution of its neighbors, because this affects its foraging area. The larger a colony’s foraging area, in which to search for seeds scattered by wind and flooding, the more likely it is to survive. The foraging trails of neighboring colonies meet about once per day (Gordon & Kulig, 1996). The larger a colony’s foraging area, the more opportunities it has to find foraging directions that do not overlap the directions taken by its neighbors. Such competition for foraging areas occurs in other ant species (Boulay et al., 2010), including other species of *Pogonomyrmex* (Ryti & Case, 1986).

Changing rainfall over the course of the study, declining after about 2001–2003 (Figure 2), has influenced the relation of colony survival and local neighborhood. The value of the foraging area appears to depend on rainfall. Rainfall is likely to be associated with food availability, because rainfall can increase seed production by the grasses and annual plants whose seeds the ants eat. In

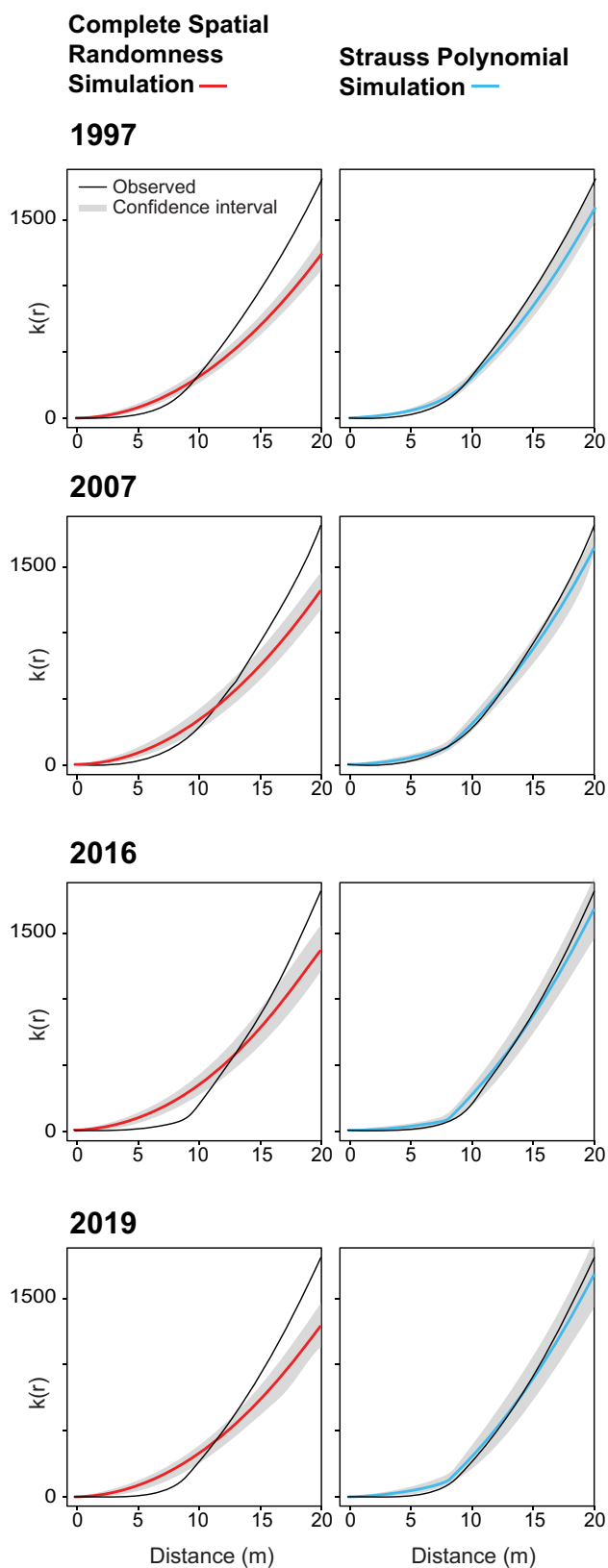


FIGURE 12 Plot of observed Ripley’s K as a function of distance for years 1997, 2007, 2016, and 2019 (see maps for these years in Figure 5). The y-axis is Ripley’s K value $k(r)$, and the x-axis is r , distance in meters. The panel on the left for each year compares the observed distribution, Ripley’s K (black line) with a random distribution (red line); the confidence interval of 95% around the null random distribution model is shown in gray. The panel on the right for each year compares the same Ripley’s K (black line) to a Strauss point process, a second order polynomial function fit to latitude and longitude, represented by a blue line at a distance r of 8 m; the confidence interval of 95% around the null Strauss polynomial model is shown in gray

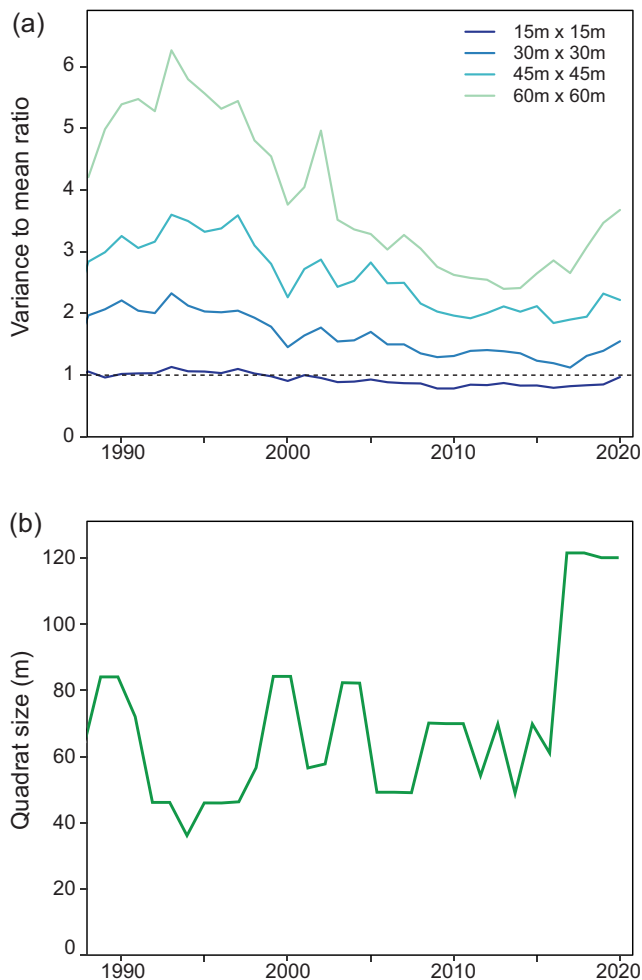


FIGURE 13 Measures of clustering. (a) Plot of variance-to-mean ratio (VMR) of nest aggregation by year. A value <1 indicates dispersion; a value >1 indicates clustering. (b) Quadrat diameter (m) at which maximum clustering occurs, by year

the earlier part of the study, from 1988 to about 2003, both rainfall and crowding were high. Throughout the Southwest United States, rainfall from 1980–1998 was higher than it had been since 1200 (Williams et al., 2020). During this time, the youngest colonies, ages 1–2 years, were most likely to survive to the following year, teens (3–4 years) and young adults (5–10 years) had similarly high chances of survival, and old colonies (more than 18 years old) were most likely to die.

Foraging area has become a more important influence on colony survival since about 2001–2003, as rainfall declined. In the southwest United States, 2000–2018 was drier than any time since 1200 (Williams et al., 2020). By about 1997–1999, the density of *P. barbatus* colonies on the site was high enough that the survival of all colonies was limited by crowding. Colony survival increasingly depended on foraging area, even though colonies had

larger foraging areas. Although crowding has decreased because the number of colonies has declined (Figures 2 and 13), the mature colonies have begun to die younger (Figures 4 and 11). We found no evidence of local crowding in the later part of the study that could account for this result (Figures 12 and 13). It seems that when rainfall is low, apparently leading to a decline in seed production by annual plants, more area is needed for a colony to find enough food. While the age of a colony's neighbors influences how they compete for foraging areas (Gordon, 1992a; Gordon & Kulig, 1996), low rainfall has a much stronger effect that outweighs that of neighbor age.

Colonies can store seeds for at least a year (Gordon, 1992a, 1993), so the effects of rainfall on food supply and survival may be lagged. Further work is needed to investigate this possibility. We found that precipitation over the entire past year had a stronger effect on recruitment than the rainfall in the current summer or the previous summer (Table 4) and we found no cumulative effect of rainfall at the 5 or 10 year scale on the survival of established colonies (Appendix S1: Table S4). These results suggest that seed production in response to both winter rain and the summer monsoons influence food availability in the current year.

Recruitment

Both rainfall and crowding are important for recruitment, because both rainfall and the spatial configuration of a founding colony's neighborhood influence the chance that it can survive to the following year. Newly mated queens disperse at random from the mating aggregation (Ingram et al., 2013). Hundreds to thousands of mated queens dig new nests at the site each year, while only a small fraction, about 5%, survive to be 1 year old. It seems that much depends on the luck of where the founding queen happens to land. Observations of newly mated queens show no evidence that the queen assesses the proximity of neighboring colonies when she chooses a site. For a founding colony to become established as a 1-year-old colony, it must be far enough away from any neighbor that it is not overrun by that neighbor's foragers. This seems to be a distance of about 8 m; the spatial scale at which colonies tend to be dispersed. Later, once a colony is established, its foraging trails can overlap with those of all of its neighbors, so that the spatial configuration of the neighborhood is important. The limiting distance of about 8 m to the nearest conspecific colony is similar to that found in an earlier study at this site during the period that rainfall was high (Gordon & Kulig, 1996). Similarly, Wiernasz and Cole (1995) found that in *P. occidentalis*, new colonies are likely to be

established if about 9 m from the nearest neighbor, leading to overdispersion on a similar spatial scale, though smaller than the mean dispersion of 18 m reported for *P. occidentalis* (Dibner et al., 2015).

It appears that the number of new colonies that survive to be 1 year old is limited by available foraging area, not by propagule availability, in numbers of reproductives the previous year. This is consistent with the previous result that alate production did not predict colony reproductive success in numbers of offspring colonies (Ingram et al., 2013). Competition for foraging area may influence propagule availability as well, as neighborhood density appeared to influence the production of alate reproductives more in 1995, following a year of lower rainfall, than in 1997 (Wagner & Gordon, 1999). The results here for *P. barbatus* differ from those of Ryti and Case (1986) or Billick et al. (2004) for other *Pogonomyrmex* species; instead it appears that, as in *Camponotus cruentatus* in southern Spain (Boulay et al., 2007), recruitment is limited by the spatial configuration of the local neighborhoods in which the newly mated queens land.

In the long term, the success of founding colonies depends mostly on rainfall. A newly founded colony is more likely to survive to be 1 year old when rainfall is high. High rainfall fueled the increase in total number of colonies from 1988 until about 1998, when rainfall was high (Figure 2). The decline in number of colonies since 1998 (Figure 2) is mostly due to the decline in recruitment as rainfall decreased (Tables 4 and 5; Appendix S1: Table S7).

The relation of rainfall and recruitment suggests that the high mortality of founding colonies is closely associated with water loss and food availability. First, the successful establishment of a 1-year-old colony is associated with precipitation in the summer that a colony is founded. The mating aggregation and colony founding take place during the summer monsoon season after heavy rain, which softens the hard caliche soil and may facilitate a founding queen's ability to dig a nest. In humid conditions, a queen may be more likely to survive a day or two outside as she flies to a mating aggregation, flies away and begins to build a nest (Johnson, 1998), and to survive the interval until her first eggs become workers that can forage. The survival of a 1-year-old colony is also associated with precipitation throughout its first year. More rainfall means higher humidity in the air and less water loss for the first foragers of the founding colony. More rainfall also means more seed production and thus higher food availability.

Our results here are consistent with, though not the same as, those of our earlier analyses of the effects of neighborhood on survival and recruitment, mostly based on data from this study before the drought began in about 2003. In an earlier study of the census data up until

1995, we found that a colony that survives to be 2 years old is likely to survive well past reproductive maturity at 5 years (Gordon & Kulig, 1998). Here we found that age-related survival shifted after about 1998, when crowding began to affect survival more and foraging area predicted survival in later years. In 2004, using data from the first 15 years of the study, 1988–2003, before the drought began, we found that mortality but not recruitment was associated with rainfall (Sanders & Gordon, 2004). Here, we found that overall recruitment was associated with rainfall. It seems that rainfall was not important for recruitment before about 2001–2003 because during that period, rainfall did not reach low enough levels to have a negative effect. Later on, when rainfall declined, it influenced survival indirectly, mediated by the extent of neighborhood crowding.

Foraging behavior, rainfall, and neighborhood

There were no persistent clusters of colonies throughout the study. It seems that there is so much variation from year to year in the spatial distribution of vegetation, and in the sources of seeds both on the site and brought in from off the site by wind and flooding, that location on the site does not strongly influence colony survival. In the earlier years of the study (e.g., around 1997–1999, Figure 2), when rainfall was high and there was more crowding, nests were clustered at about 12–16 m (Figures 5 and 12). After 1997–1999, as rainfall and number of colonies decreased, nests were somewhat more dispersed, with some evidence of clustering at larger scales above about 12–16 m along with strong overdispersion at small spatial scales of 8 m (Figures 5 and 12). This is similar to the results of (Dibner et al., 2015) for *P. occidentalis*, on a much larger spatial scale, showing increased overdispersion as rainfall decreased.

In dry conditions, how a colony regulates foraging behavior so as to manage water loss may influence its survival. The effects of foraging area do not fully explain survival (Figure 8, Table 3). As rainfall has decreased, for example, in the break-point year of 2016, the foraging areas of young adult colonies that died were not generally smaller than those of colonies that survived (Figure 10). Colonies differ in the collective regulation of foraging activity in response to water loss (Gordon, 2013; Gordon et al., 2011). Some colonies are more likely than others to reduce foraging activity in dry conditions, thus sacrificing food intake to conserve water. In an analysis performed in 2010 for colonies most active from 1995 to 2010, the colonies that conserve water by reducing foraging in dry conditions were more likely to have offspring colonies than

those that did not reduce foraging in dry conditions (Gordon, 2013). These differences among colonies are associated with differences in sensitivity to water loss (Friedman et al., 2019), and in the role of dopamine in the behavior that regulates foraging activity (Friedman et al., 2020).

Variation among colonies in foraging behavior affects the interactions of neighboring red harvester ant colonies (Cole & Wiernasz, 2002; Gordon & Kulig, 1996; Lubertazzi et al., 2013). How a colony regulates foraging activity in response to water loss may indirectly affect its survival through its effects on competition with neighbors. As the drought has deepened, mortality has increased in younger adult colonies. It may be that as rainfall declines, and food becomes scarcer, the regulation of foraging activity so as to reduce water loss may have more impact on colony survival. This may be especially true for a colony living in a crowded neighborhood that constrains its foraging area. Although the colony can conserve water on dry days by reducing foraging, on humid days all colonies tend to be active. The more crowded the neighborhood, the more the foraging activity of that colony's neighbors limits the amount of food it can gather. If a colony's foraging area is too small, when it extends its foraging activity on a humid day, it faces more encroachment from its neighbors who are likely to be active on that day as well. In the 10–15 years up until 2010, the colonies that sacrificed food intake to conserve water, by reducing foraging activity in dry conditions, were more likely to have offspring colonies (Gordon, 2013). However, it may be that as the drought has deepened, the food supply has become low enough that crowded colonies cannot afford to sacrifice food intake without compromising their survival.

Our results contribute to the growing literature on the diversity of ecological processes that regulate the spatial distributions and dynamics of populations of ant colonies, reflecting the diversity of conditions in which different species evolved (Adams, 2001; Dong, 2020; Gordon, 2019). Ant species differ greatly in the extent of intraspecific aggression, which may be sustained and frequent, as in the fire ant *Solenopsis invicta* (Adams & Tschinkel, 1995), or rare and episodic as in the *P. barbatus* population described here (Gordon & Kulig, 1996). Species with a single nest per colony also differ greatly in the extent to which colonies tolerate overlap with their neighbors in foraging ranges; for example, from the large overlap in *Camponotus cruentatus* (40%) (Boulay et al., 2007) to those created by foraging trails in *P. barbatus* (Gordon & Kulig, 1996) and other *Pogonomyrmex* species (Ryti & Case, 1992; Wiernasz & Cole, 1995). Species that have many nests

per colony, or reproduce by colony fission, show even more diversity in interactions with neighbors (Chen et al., 2018; Tanner & Keller, 2012; van Wilgenburg & Elgar, 2007). The rate at which populations of colonies adjust to shifts in density, which may depend on rates of resource renewal and on propagule availability (Cole & Wiernasz, 2002; Tanner & Keller, 2012), ranges from very high as in *Aphaenogaster senilis* (Boulay et al., 2010), in which density recovered from experimental removals after one reproductive season, to the slow responses reported here for *P. barbatus*, which play out over decades.

Climate change

The processes at the scale of local neighborhoods that link density and population dynamics in a population of *P. barbatus* colonies reflect the evolution of foraging behavior in an environment in which resource availability changes slowly (Gordon, 2019). However, climate change is rapidly altering the conditions that affect food availability and foraging activity, which are both strongly dependent on rainfall.

Will this population survive as climate change continues and the southwestern United States becomes increasingly dry? Sustained drought has species-specific effects at different time scales (e.g., for birds [Cady et al., 2019] and plants [Bachelot et al., 2020]), and can lead to local extinction (Panetta et al., 2018). Climate change, including drought, leads to declines in insect populations (Halsch et al., 2021), altering the spatial distribution of ant species (Couper et al., 2021) and the trophic structure of insect communities (Zhu et al., 2014). It is an open question whether some species have the adaptive capacity to respond quickly enough to rapid and drastic ecological shifts caused by climate change (Beever et al., 2017; Palumbi et al., 2014). In *P. barbatus*, selection for the collective regulation of foraging that conserves water may be intense enough to promote behavioral phenotypes that can persist. Climate change is shaping the evolution of the behavior that mediates interactions among neighbors that determine how resource competition responds to changing density.

ACKNOWLEDGMENTS

We are very grateful to Maria Joao Ferreira Santos for her conceptual contributions and statistical analysis for an earlier version of this project. We thank Shripad Tuljapurkar, Fred Adler, and Robert K. Swihart for valuable discussions about the statistical analysis. The comments of anonymous reviewers greatly improved the

manuscript. We would like to express our appreciation to many cohorts of research assistants. Unfortunately, the data recording procedures for ant colonies were much better than those for recording the names of all of the about 50 undergraduates who have contributed to the fieldwork over the years, but we thank them all. DMG would especially like to acknowledge the enthusiastic contributions of the late Victoria Braithwaite, who worked on this project in the summer of 1989 when she was an undergraduate at Oxford. LeAnn Howard has contributed greatly to this project for many years, both in helping with fieldwork and interesting discussions. The work has benefited enormously from Sam Crow's many years of work on the census, including software for data collection and for navigating the site. We would also like to thank many successive directors and the staff at the Southwestern Research Station for their help and support. Our recent work on this project has been supported by grants to DMG from the Hewlett Fund, National Science Foundation 1940647, and the Templeton Fund. M. Sundaram led the design of the statistical analysis, performed all statistical analyses, and contributed to the writing of the manuscript. E. Steiner created the database, performed the data visualization, and contributed to the writing of the manuscript. D. Gordon conceived, maintained, and supervised the project, collected or supervised the collection of the data, and led the writing of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Sundaram et al., 2022) are available from the Stanford Data Repository: <https://doi.org/10.25740/sz403bn0186>.

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How to cite this article: Sundaram, Mekala, Erik Steiner, and Deborah M. Gordon. 2022. "Rainfall, Neighbors, and Foraging: The Dynamics of a Population of Red Harvester Ant Colonies 1988–2019." *Ecological Monographs* e1503. <https://doi.org/10.1002/ecm.1503>