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SHORT COMMUNICATION

The interactive effects of climate, life history, and interspecific neighbours on mortality in a population of seed harvester ants

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Abstract. 1. Fifteen years of census data from a population of the red harvester ant (*Pogonomyrmex barbatus*), 5 years of census data from populations of *Aphaenogaster cockerelli* and *Myrmecocystus mimicus* at the same site, and long-term precipitation data from a nearby weather station were used to examine how nearest interspecific neighbours, climate, and life history influence *P. barbatus* colony mortality.

2. It was found that more *P. barbatus* colonies die following dry summers than following wet summers, but there is no relationship between the establishment of new colonies and rainfall.

3. *Aphaenogaster cockerelli*, but not *M. mimicus*, nearest neighbours influence *P. barbatus* colony mortality in some years and for some ages.

4. The effects of nearest *A. cockerelli* neighbours are usually most severe following dry summers, when resource availability is reduced.

Key words. Ant populations, climate, competition, desert, life history, seed harvester.

Introduction

Both biotic and abiotic factors influence the dynamics of consumer populations. The demographic effects of biotic factors may depend on life history. To link climatic fluctuation to population dynamics, long-term data are needed. Unfortunately, such data are rare (though see, for example, Polis *et al.*, 1998; Grant & Grant, 2003), especially for ant populations. How rainfall, life history, and proximity to nearest interspecific neighbours are examined here to see how they contribute to the dynamics of a population of the red seed harvester, *Pogonomyrmex barbatus* (F. Smith).

Rainfall affects the abundance of many populations (e.g. Brown, 1987; Sala *et al.*, 1988; Polis *et al.*, 1998; Lima *et al.*, 1999; Ernest *et al.*, 2000; Kaspari & Valone, 2002). Rainfall is positively correlated with pulses of seed resources in deserts in south-western U.S.A. (Kemp, 1989; Ernest *et al.*, 2000), and both seed abundance and rainfall can vary dramatically from year to year (Kemp, 1989). Neighbouring colonies of seed-eating ants compete for food when they search overlapping areas. Interactions with neighbours affect the intensity and location of foraging (Gordon, 1992; Sanders & Gordon, 2000, 2003), establishment of new colonies (Hölldobler, 1976; Majer, 1976; Chew, 1987; Ryti & Case, 1988; Gordon & Kulig, 1996; Jerome *et al.*, 1998; Adams & Tschinkel, 2001), mortality (Adams & Tschinkel, 1995; Gordon & Kulig, 1998), and the production of reproductives (Pontin, 1961; Gordon & Wagner, 1997).

The intensity of competition varies with life-history stage (Rajapakse *et al.*, 1992; Nisbet & Onyiah, 1994; Krebs & Barker, 1995). Life history influences population dynamics and interactions with neighbours because behaviour changes as individuals grow or age. In ants, colony age influences interactions with neighbours and population dynamics. For example, young *Oecophylla longinoda* colonies may recruit more workers to territorial borders than do older colonies (Hölldobler & Wilson, 1978). Intermediate-aged *P. barbatus* colonies, before they reach reproductive age, are more persistent in competition with their *P. barbatus* neighbours than are younger colonies or older,

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mature ones (Gordon, 1991, 1992). The intensity of interactions between of *P. barbatus* and one of its competitors, *Aphaenogaster cockerelli*, changes as the *P. barbatus* colony matures (Barton *et al.*, 2002).

Patterns of interspecific spacing, using average nearest-neighbour distances, reveal interesting spatial associations between species in many desert ant species (Hölldobler, 1981; Bernstein & Gobbel, 1979; Chew, 1987; Ryti & Case, 1984; Cole & Wiernasz, 2001). In this study, 15 years of census data from a population of the red harvester ant (*Pogonomyrmex barbatus*), 5 years of census data from populations of *Aphaenogaster cockerelli* (André) and *Myrmecocystus mimicus* (Wheeler) at the same site, and long-term climate data from a nearby weather station are used. Previous work on the *P. barbatus* population at this site has shown that the density of intraspecific neighbours influences the probability of mortality for newly founded colonies but has little effect on older, well-established colonies (Gordon & Kulig, 1996; Gordon & Kulig, 1998). Here, the effect of interspecific neighbours on the probability of mortality of newly founded and older colonies is focused on. Specifically, four related questions about mortality and the establishment of new colonies in *P. barbatus* are asked:

1. What is the effect of amount of precipitation on colony mortality and the establishment of new colonies?
2. What is the effect of proximity to nearest interspecific neighbours on colony mortality?
3. Do the effects of precipitation and neighbour proximity interact?
4. Do the effects of precipitation and neighbour distance depend on colony age?

Methods

Pogonomyrmex barbatus colonies compete with other ants, birds, and rodents for seeds (Davidson, 1977). New colonies are founded by a single queen that mated in the previous year's mating flight. A colony reaches maturity, producing reproductives, when it is about 5 years old (Gordon, 1995) and has about 10 000 workers (Gordon, 1992). The colony remains at this size for another 10–15 years (Gordon & Kulig, 1998). The colony dies once the queen has died, and all of the remaining workers, who have a lifespan of about a year (Gordon & Hölldobler, 1987) have eventually died; new queens are not adopted into existing colonies.

Every *P. barbatus* colony at a 10-ha site near Rodeo, New Mexico has been mapped, censused and labelled every summer since 1985 (for details of the censusing method, see Gordon, 1987, 1991, 1992, 1995). For most new colonies established on the site since 1985, the age is known. In 1985 the ages of some colonies were estimated to be 5 years or older based on comparisons with the sizes of nests of known age. In this study three life-history stages are distinguished: young, intermediate (3–4 years old before reproductive age), and mature (5 years or older, past the age when reproduction begins). A colony is considered to be dead when the nest entrance is closed, the mound is overgrown with vegetation, and no ants emerge from the nest entrance after prodding it with a twig on at least five different days.

Each summer from 1997 to 2001, *A. cockerelli* and *M. mimicus* colonies were mapped and labelled on the site using methods similar to those used for the *P. barbatus* population. *Aphaenogaster cockerelli* colonies can form polydomous colonies of one to five nests. To determine which *A. cockerelli* nests belonged to which colonies in areas of high nest density, aggression tests were often conducted by introducing a worker from one nest within 10 cm of the entrance of another active nest. At least five introductions for each pair of nests were performed in high density areas. The nest of the introduced worker was considered to belong to another colony if the workers fought or moved quickly away from each other in any of the five trials. Nests were considered to belong to the same colony when they were near each other and separated from other *A. cockerelli* nests by about 30 m. For the analyses described below, the centroid of all the nest locations was used as the location of the *A. cockerelli* colony. *Myrmecocystus mimicus* colonies have one nest per colony. It is not clear which populations of *P. barbatus* in this area of the south-western U.S. have hybridised with *P. rugosus* (Volny & Gordon 2002; Julian *et al.*, 2002; Helms Cahan & Keller, 2003).

To examine the relationship between precipitation and *P. barbatus* mortality and the establishment of new colonies, census and climate data from 1988 to 2002 were used. To estimate mortality for each year, the number of colonies that died in the year prior to the census were tallied, and to estimate colony establishment, the number of 1-year-old colonies were used. Precipitation at the site was estimated from a long-term weather station approximately 10 km from the site (data available on line: http://www.wrcc.dri.edu). Most precipitation events in the south-western U.S.A. occur during two distinct periods: winter (December to February) and summer (July to August). Winter rainfall triggers seed set in March and April, and summer rainfall triggers seed set in August and September. *Pogonomyrmex barbatus* mortality and establishment of new colonies were correlated with winter and summer rainfall in the previous year to assess the response to both periods of seasonal rainfall. Mortality, colony establishment, and summer precipitation were not positively or negatively serially correlated among years (Durbin–Watson analysis, $P > 0.05$ in all cases), indicating that increases and decreases did not occur in runs.

Multiple logistic regression was used to examine the effects of colony life history and distance to neighbours on *P. barbatus* colony mortality from 1997 to 2002. In all of the models, the response variables consisted of either 1s (the colony lived till the next year) or 0s (the colony was dead by the next year). In all of the models, distance to the nearest *M. mimicus* or *A. cockerelli* colony was $\log(n+1)$ transformed

Table 1. Spearman rank correlation coefficients between seasonal precipitation, *Pogonomyrmex barbatus* colony mortality, and colony establishment.

Variable 1	Variable 2	r_s	P
Winter precipitation	Mortality	−0.41	0.13
Winter precipitation	Establishment	0.01	0.98
Summer precipitation	Mortality	−0.28	0.31
Summer precipitation	Establishment	−0.03	0.90
Summer precipitation in previous year	Mortality	−0.56	0.03
Summer precipitation in previous year	Establishment	0.23	0.40
Mortality	Establishment	0.26	0.34

to improve normality. The effects of proximity to the nearest *A. cockerelli* colony, year, and *P. barbatus* colony life-history stage on the probability that the *P. barbatus* colony died by the next year were examined. The same was then done for the effect of *M. mimicus* on *P. barbatus* mortality.

Logistic regression assumes that observations are independent of one another. Whether a colony is alive in a given year clearly depends on whether that colony was alive or dead at the beginning of that year. Nevertheless, the observations across years are independent of one another because the probability that a colony dies in a particular year is being examined, given that it is alive at the beginning of that year.

Results and Discussion

Pogonomyrmex barbatus colony mortality is related to rainfall from the previous summer. Years with high mortality are usually preceded by dry summers (Table 1, Figs 1 and 2). Winter and summer rainfall during the year of the census are not related to mortality (Table 1). Establishment of new colonies was not related to winter or summer rainfall in the same year (Table 1). But heavy rainfall during the El Niño summer of 1999 probably led to high levels of mortality for many newly established colonies.

The precipitation data suggest that the March to April seed set triggered by winter rainfall has little effect on *P. barbatus* colonies at the site. Kaspari and Valone (2002) found that the abundance of four granivorous ant species at a site near the one studied in the work reported here was positively correlated with summer but not winter rainfall. These results, which are similar to Kaspari and Valone's, highlight that rainfall-triggered resource availability influences mortality, but increased seed set following summer precipitation does not lead to higher colony production. Kaspari and Valone (2002) suggest that low winter and early spring temperatures limit colonies' access to the early seed set triggered by winter rainfall. Most *Pogonomyrmex* colonies are rarely active until June (Whitford & Ettershank, 1975), probably after the early seed set has been harvested by rodents and other granivores.

Mortality was generally lowest from 1988 to 1992, following summers when precipitation was above average (Fig. 1). Mortality was highest following the dry summers of 1994–1998. The number of new colonies on the site appeared not to be influenced by summer precipitation, except in 1999 when the site flooded. Colony mortality was also highest during 1999, probably because colonies flooded, and new colonies were especially susceptible because their seed stores were too near the soil surface.

The proximity of interspecific neighbours also influenced *P. barbatus* mortality. *Aphaenogaster cockerelli* nearest neighbours influenced *P. barbatus* colony mortality in some years and for some ages (Table 2, Fig. 3), but *M. mimicus* nearest neighbours did not (Table 2). The *A. cockerelli* model across all years showed strong effects of year ($P = 0.04$), *P. barbatus* colony age ($P = 0.01$), and a colony age × distance interaction ($P = 0.05$). The distance effect ($P = 0.09$) by itself and the year × distance interaction ($P = 0.06$) were marginally insignificant. The significant year effect suggests that colonies are more likely to die in some years than in others, and the age effect simply shows

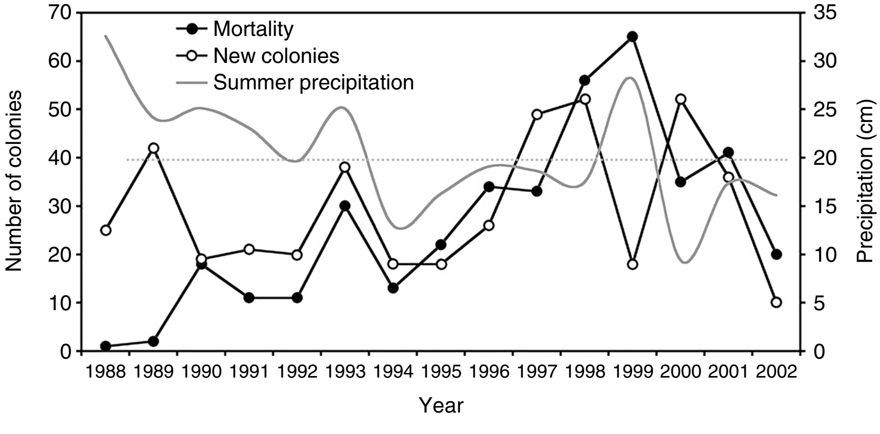

Fig. 1. Variation in summer precipitation, mortality, and the establishment of new colonies at the site near Rodeo, New Mexico. The horizontal dashed line indicates the 20-year average amount of summer precipitation.

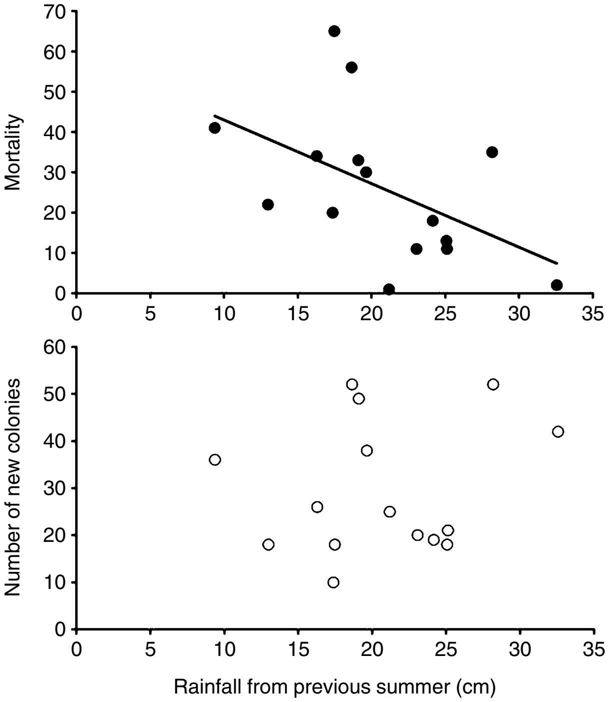

Fig. 2. The relationship between precipitation during the previous summer and colony mortality and establishment.

that colonies are more likely to die as they get older (Gordon & Kulig, 1998).

The year × distance to *A. cockerelli* effect on *P. barbatus* mortality shows that the effect of *A. cockerelli* on *P. barbatus* varied among years. *Pogonomyrmex barbatus* colonies that survived from 1997 to 1998 were, on average, 5 m closer to the nearest *A. cockerelli* neighbour than those that did not survive (Fig. 3). *Pogonomyrmex barbatus* colonies that survived from 2000 to 2001, in contrast, were 4 m farther from their *A. cockerelli* nearest neighbour. This suggests that interactions between *P. barbatus* and *A. cockerelli* switched from positive in 1997 to negative in 2000. This appears to be influenced by rainfall. *Aphaenogaster cockerelli* has a negative effect on *P. barbatus* survivorship after dry summers (2000), when resource availability is reduced. There is considerable year-to-year variation in seed supply in the deserts of the south-western U.S.A. (Kemp, 1989), and this probably depends on rainfall. Summer rainfall in 1996 and 1997 did not significantly differ from the long-term (1980–2002) average rainfall (one-sample t-test, 1996: $t_{21} = 0.84$, $P = 0.40$; 1997: $t_{21} = 1.23$, $P = 0.23$), and rainfall in 1998 was only slightly less than average ($t_{21} = 2.175$, $P = 0.04$). In 1996, 1997, and 1998, *A. cockerelli* did not negatively affect *P. barbatus* (Fig. 3). In 1999, there was severe flooding, which probably deterred foraging by both species and may have obscured the effect of competition. However, 2000 was the driest year since the census began, and *A. cockerelli* had

Table 2. Summary statistics from logistic regression analysis on the effects of year, *Pogonomyrmex barbatus* colony age, distance to nearest interspecific neighbours, and their interactions on *P. barbatus* colony mortality.

Effect	d.f.	Wald χ^2	P
The effect of *Aphaenogaster cockerelli*			
Year	4	10.15	0.04
P. barbatus colony age	1	6.81	0.01
Year × *P. barbatus* colony age	4	6.12	0.19
Distance to *A. cockerelli*	1	2.87	0.09
Year × distance to *A. cockerelli*	4	8.93	0.06
P. barbatus colony age × distance to *A. cockerelli*	1	3.67	0.05
Year × *P. barbatus* colony age	4	5.50	0.24
The effect of *Myrmecocystus mimicus*			
Year	4	6.54	0.16
P. barbatus colony age	1	5.29	0.02
Year × *P. barbatus* colony age	4	7.51	0.11
Distance to *M. mimicus*	1	2.24	0.13
Year × distance to *M. mimicus*	4	6.10	0.19
P. barbatus colony age × distance to *M. mimicus*	1	2.90	0.11
Year × *P. barbatus* colony age	4	6.99	0.14

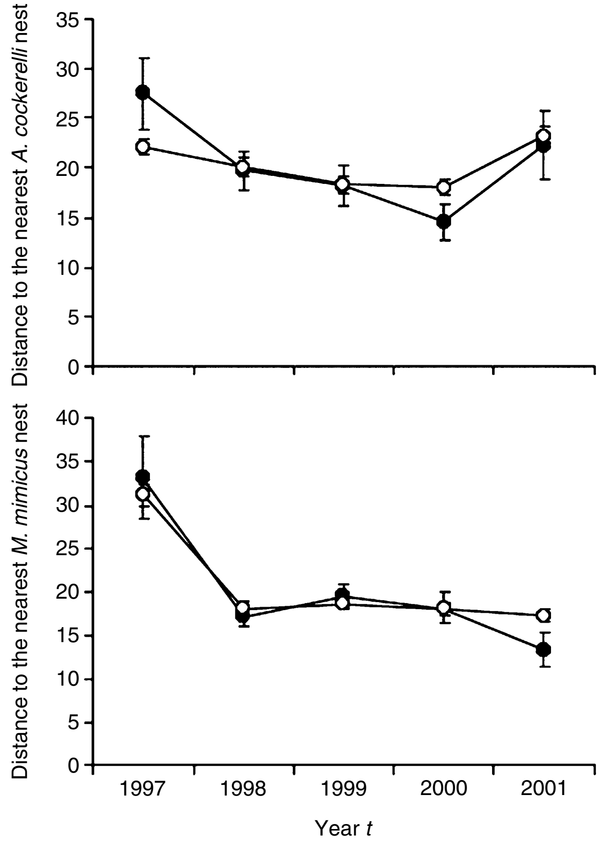

Fig. 3. The effects of nearest neighbours on *Pogonomyrmex barbatus* colony mortality during 5 years of study. Symbols indicate mean distance (m) to the nearest neighbour (±SEM) in year t. ●, Colonies that died in year $t+1$; ○, colonies that lived to year $t+1$.

a strong negative effect on *P. barbatus*; colonies closer to *A. cockerelli* nearest neighbours were less likely than more distant ones to persist to 2001.

The effect of *A. cockerelli* on *P. barbatus* includes interference as well as exploitative competition. *Aphaenogaster cockerelli* colonies sometimes plug the nest entrances of neighbouring *P. barbatus* colonies. This plugging deters or delays *P. barbatus* colony activity (Gordon, 1988). Barton *et al.* (2002), following two summers with average rainfall, found that nearby *P. barbatus* colonies, less than 10 m from an *A. cockerelli* nest, were plugged almost 2.5 times as frequently as colonies with more distant *A. cockerelli* neighbours at least 10 m away.

The positive effect of *A. cockerelli* on *P. barbatus* survival (from 1997 to 1998) warrants further study. In a similar study, Cole and Wiernasz (2001), showed that *Myrmecocystus mexicanus* nests are positively associated with nests of the western seed harvester, *Pogonomyrmex occidentalis*, in Colorado. They suggest that this positive association arises because the main source of available food to *M. mexicanus* is *P. occidentalis*. This hypothesis was not explicitly tested to explain why *P. barbatus* colonies had a higher probability of surviving when they were near *A. cockerelli* (from 1997 to 1998), because *P. barbatus* does not use *A. cockerelli* as a food source.

The effect of *A. cockerelli* on *P. barbatus* mortality depended on *P. barbatus* colony age, as indicated by the significant colony age × distance interaction in Table 2. Previous work showed that competitive interactions with *A. cockerelli* depend on the age of *P. barbatus* neighbours: *A. cockerelli* colonies plug 1–2-year-old *P. barbatus* colonies 1.4 times as frequently as they do colonies older than 2 years, and the distance between the *A. cockerelli* colony and the young *P. barbatus* colony does not influence the frequency of plugging (Barton *et al.*, 2002). *Aphaenogaster cockerelli* does not affect the probability of dying in young (1–2 years) or intermediate (3–4 years) aged *P. barbatus* colonies (Fig. 4). But for old colonies (>5 years), being close to *A. cockerelli* increases the probability of dying (Fig. 4).

The population dynamics of *P. barbatus* depend on year-to-year variation in summer rainfall, the impact of both intraspecific (Gordon & Kulig, 1996, 1998) and interspecific interactions (Gordon, 1988; Barton *et al.*, 2002), and life history. How do climate, colony age, and interactions from *A. cockerelli* interact to influence *P. barbatus* colony mortality? Intraspecific competition by well-established neighbours strongly influences the survival of founding colonies (Gordon & Kulig, 1996, 1998), but has little effect on the survival of older ones. The results from the work reported here suggest that interspecific competition may influence the mortality of older colonies in years when low rainfall limits food availability. It may be that the queen is more likely to succumb to adverse conditions when she is older (Orzack & Tuljapurkar, 1989). These long-term data suggest that the dynamics of this population are mediated by multiple biotic and abiotic factors and depend on life-history characteristics.

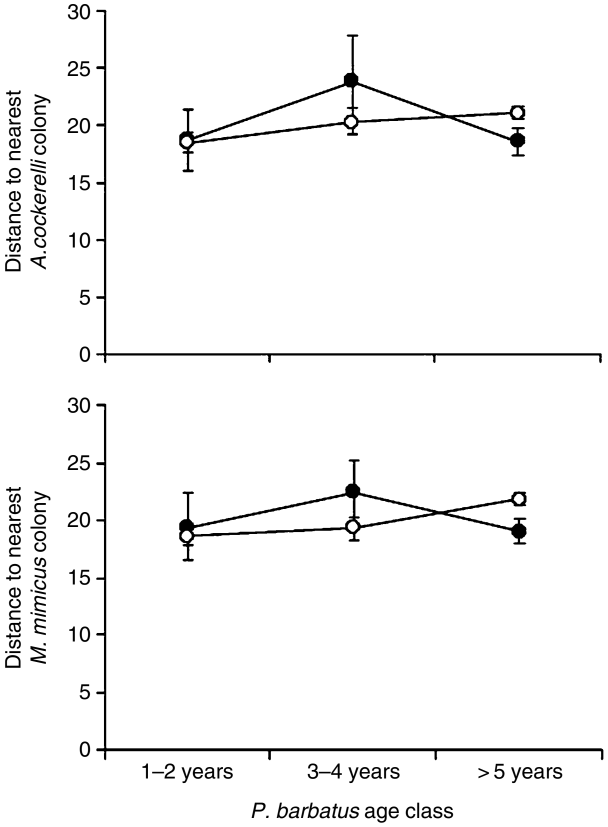

Fig. 4. The effects of nearest neighbours on *Pogonomyrmex barbatus* colony mortality in each age class. Symbols indicate mean distance (m) to the nearest neighbour (±SEM). ●, Colonies that died; ○, colonies that lived.

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