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The Effects of Proximity and Colony Age on Interspecific Interference Competition between the Desert Ants Pogonomyrmex barbatus and Aphaenogaster cockerelli

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ABSTRACT.—The ants *Aphaenogaster cockerelli* and *Pogonomyrmex barbatus* compete for seed resources in the Chihuahuan desert. Previous work showed that intraspecific competition in *P. barbatus* is more intense between near neighbors with overlapping foraging ranges and depends on colony age. Just before reaching reproductive maturity (3–4 y), colonies are more aggressive and persistent in intraspecific competition for foraging area than younger or older colonies. In this study we examine how interspecific interference behavior by *A. cockerelli* towards *P. barbatus* depends on the age and proximity of *P. barbatus* colonies. Before sunrise when *P. barbatus* colonies become active, *A. cockerelli* colonies completely plug the nest entrances of some *P. barbatus* colonies, thereby delaying the onset of *P. barbatus* foraging behavior. *Pogonomyrmex barbatus* colonies closer to *A. cockerelli* were plugged more frequently than more distant colonies. As distance from *A. cockerelli* nests increased, older *P. barbatus* colonies were plugged more frequently than younger ones. Our results suggest that the intensity of interspecific interference competitive interactions may depend on the proximity and age of competing colonies.

INTRODUCTION

For many organisms, there are both spatial and life-history effects on competition (Tschumy, 1982; Pacala and Silander, 1985; Siegismund *et al.*, 1990; Tilman and Kareiva, 1997). For example, the intensity of competition may depend on density of individuals, and the resource use and behavior of competing individuals may change as they grow older or larger (Werner and Gilliam, 1984; Stamps and Eason, 1989).

In ants, there have been numerous studies on the relationship between the spatial distribution of colonies and competition (*e.g.*, Hölldobler, 1976; Levings and Traniello, 1981; Ryti and Case, 1984, 1986, 1988). Some studies invoke competition as the cause of regular spacing patterns among colonies (*e.g.*, Levings and Traniello, 1981) and others estimate the intensity of competition by measuring the distances among colonies (*e.g.*, Ryti and Case, 1986). The distance between colonies may be negatively correlated with the intensity of interactions: short distances to nearest neighbors and overlapping foraging areas may increase the probability of competitive interactions (Hölldobler, 1981; Gordon and Kulig, 1996) and colony mortality (Thurber *et al.*, 1993). However, some studies show a positive correlation between interaction intensity and distance between colonies (*e.g.*, Heinze *et al.*, 1996; Langen *et al.*, 2000).

It is difficult to study life-history effects on behavioral interactions in ant communities because long-term data are needed to determine the ages of individual colonies. Evidence

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suggests that newly founded colonies of several species are less likely to survive when they are located near older established neighbors (Hölldobler, 1981; Chew, 1987; Ryti and Case, 1988; Adams and Tschinkel, 1995; Wiernasz and Cole, 1995; Gordon and Kulig, 1996, 1998). In some species behavior changes as colonies grow older. For example, in the African weaver ant, *Oecophylla longinoda*, young colonies may recruit more workers to contested territorial borders than do older colonies (Hölldobler, 1978). In the red harvester ant, *Pogonomyrmex barbatus*, colony behavior depends on colony age: intermediate-aged colonies (3–4 y old) are more persistent in intraspecific conflicts over foraging area than are younger or older colonies (Gordon, 1991, 1992).

In this study we test how the probability that a *Pogonomyrmex barbatus* colony is subject to interference from *Aphaenogaster* (=*Novomessor*) *cockerelli* depends on the age of the *P. barbatus* colony and on its distance from a nest of *A. cockerelli*. *Aphaenogaster cockerelli* and *P. barbatus* compete for seed resources (Davidson, 1977). *Aphaenogaster cockerelli* colonies, which are active throughout the night and into the morning (Whitford and Ettershank, 1975), sometimes plug the nest entrances of neighboring *P. barbatus* colonies with pebbles and bits of soil before sunrise when *P. barbatus* becomes active (Gordon, 1988). Nest-plugging delays the onset of the daily activity of a *P. barbatus* colony and thus reduces the time it spends foraging; this could leave more resources available for the *A. cockerelli* colony. Here we ask if the frequency with which *P. barbatus* colonies are plugged by *A. cockerelli* depends on *P. barbatus* colony age and its distance to the nearest *A. cockerelli* neighbor.

MATERIALS AND METHODS

We conducted this study in the Chihuahuan desert near Rodeo, New Mexico (31°50′N 109°102′W). *Aphaenogaster cockerelli* and *Pogonomyrmex barbatus*, along with other granivorous rodents and birds, compete for seed resources (Davidson, 1977; Brown, 1998). Both species also collect insect prey (Hölldobler *et al.*, 1978; Chew and De Vita, 1980; Whitford *et al.*, 1980; Sanders and Gordon, 2000), though *P. barbatus* relies heavily on seeds (Gordon, 1993). *Aphaenogaster cockerelli* is active from sunset to mid-morning (Whitford and Ettershank, 1975) and *P. barbatus* is generally active from sunrise until about noon and again in the early evening. The activity periods of the two species overlap for several hours.

One of us (DMG) has mapped and censused the *Pogonomyrmex barbatus* population on the site every summer since 1985 (for details, *see* Gordon and Kulig, 1996). Each colony is individually labeled and located by coordinates from a fixed origin using a Wild infrared theodolite. In 1985 some colonies were estimated to be 5 y or older by comparison with nests of known age. Since 1985 the age of most new colonies established on the site is known. *Pogonomyrmex barbatus* colonies last for 15–20 y (Gordon, 1991), occupying a single nest. Colonies are considered to be 1-y old, founded from the previous year's mating flight, the summer they are first included in the census.

Since the summer of 1997 we have mapped and censused every *Aphaenogaster cockerelli* colony on the site. *Aphaenogaster cockerelli* colonies can form polydomous colonies of 1–5 nests and each nest of each colony is individually labeled and located using the theodolite. To determine which nests belonged to which colonies in areas of high nest density, we conducted aggression tests by introducing a worker from one nest within 10 cm of the entrance of another active nest mound. We performed at least five introductions for each pair of nests in high density areas. The nest of the introduced worker was considered to belong to another colony if the workers fought or hurried away from each other in any of the five trials.

We examined if nest-plugging of *Pogonomyrmex barbatus* by *Aphaenogaster cockerelli* depends on *P. barbatus* age and distance to the nearest *A. cockerelli* colony. We visited 27 colonies each morning for 10 d in 1998 and 46 colonies each morning for 17 d in 1999. Observations began at approximately 0600, and we visited colonies in a haphazard order. We considered a nest to be plugged if it had small rocks and sticks in the entrance or if *P. barbatus* workers were actively removing rocks and sticks from the nest entrance. If we saw *P. barbatus* workers removing rocks from the interior of the nest, we did not count the nest as plugged. A previous study indicated that some *P. barbatus* colonies may infrequently plug their own nests to maintain soil humidity, but usually only when conditions are dry. That study also showed that most plugging resulted from the activity of neighboring *A. cockerelli* colonies (Gordon, 1988), and we occasionally witness *A. cockerelli* workers plugging *P. barbatus* colonies.

We tallied the proportion of days each *Pogonomyrmex barbatus* colony in our study was plugged out of all days that it was observed. Because some colonies were never plugged, we also performed analyses on the subset of colonies that were plugged at least once. To determine the effect of age and distance to the nearest *Aphaenogaster cockerelli* neighbor on the probability of *P. barbatus* colony's being plugged, we classified colonies as young (1–2 y), intermediate aged (3–4 y) and old (>4 y) and near (<10 m) and far (>10 m) and used a two-way ANOVA with age and distance class as the main effects in the model, and the arcsin-transformed proportion of days as the response variable. For the analysis, we used the age of the colony at the time observations were made on it. We also used the distance to the nearest neighbor during the year observations were made. For example, for a *P. barbatus* colony in 1998, we counted the number of days it was plugged out of 10, and determined its age and the distance to its nearest *A. cockerelli* neighbor. To calculate the distance to an *A. cockerelli* colony with more than one nest entrance, we used the average of all the x and y coordinates as the colony's location because *A. cockerelli* workers could come from any nest entrance, not just the closest one, to plug a nest. The distance between our focal *P. barbatus* colonies and their nearest *A. cockerelli* neighbors ranged from 0.3 m to 49.0 m.

RESULTS

There was a significant effect of distance to the nearest *Aphaenogaster cockerelli* neighbor on the frequency with which *Pogonomyrmex barbatus* colonies were plugged (Table 1). When we examined all of the data from all colonies, there was no effect of *P. barbatus* colony age (Table 1). When we examined the data from only the *P. barbatus* colonies that were plugged at least once, closer colonies were significantly more likely to be plugged than distant colonies (Table 1). The interaction between colony age and distance to *A. cockerelli* was significant (Fig. 1, Table 1), indicating that colony age and proximity to the nearest *A. cockerelli* colony are not independent of one another. When close to *A. cockerelli*, young colonies were more likely than intermediate-aged ones to be plugged. But when distant from *A. cockerelli*, intermediate-aged colonies were more likely than young ones to be plugged. Older colonies were plugged at roughly the same frequency at all distances.

DISCUSSION

Any *Pogonomyrmex barbatus* colony that was plugged at least once was plugged frequently, on about 1 out of every 5 d we made observations. Nest-plugging at this frequency may affect the amount of food resources colonies collect, and ultimately their fitness. When a colony is plugged, the onset of activity is delayed. In *P. barbatus*, foraging is the last activity to be performed in a daily sequence of activities (Gordon, 1984). If the onset of activity is

TABLE 1.—Analysis of variance of proportion of days *Pogonomyrmex barbatus* were plugged

Source	df	SS	*F*	*P*
All colonies (n = 73)				
Age	2	0.114	1.87	0.161
Distance	1	0.422	13.92	0.0004
Age × Distance	2	0.157	2.59	0.082
Error	67	2.029		
Colonies plugged at least once (n = 48)				
Age	2	0.002	0.29	0.746
Distance	1	0.284	9.17	0.004
Age × Distance	2	0.218	3.51	0.039
Error	42	1.30		

delayed, foraging behavior may not begin until later in the day, when soil surface temperatures restrict colony activity. *Pogonomyrmex barbatus* colonies do not compensate for lost time by increasing foraging intensity (Gordon, 1988).

Aphaenogaster cockerelli did not plug all *Pogonomyrmex barbatus* colonies with the same frequency; nearby colonies were plugged more frequently than distant colonies. Perhaps *A. cockerelli* colonies plug the nests of *P. barbatus* colonies with which they compete most

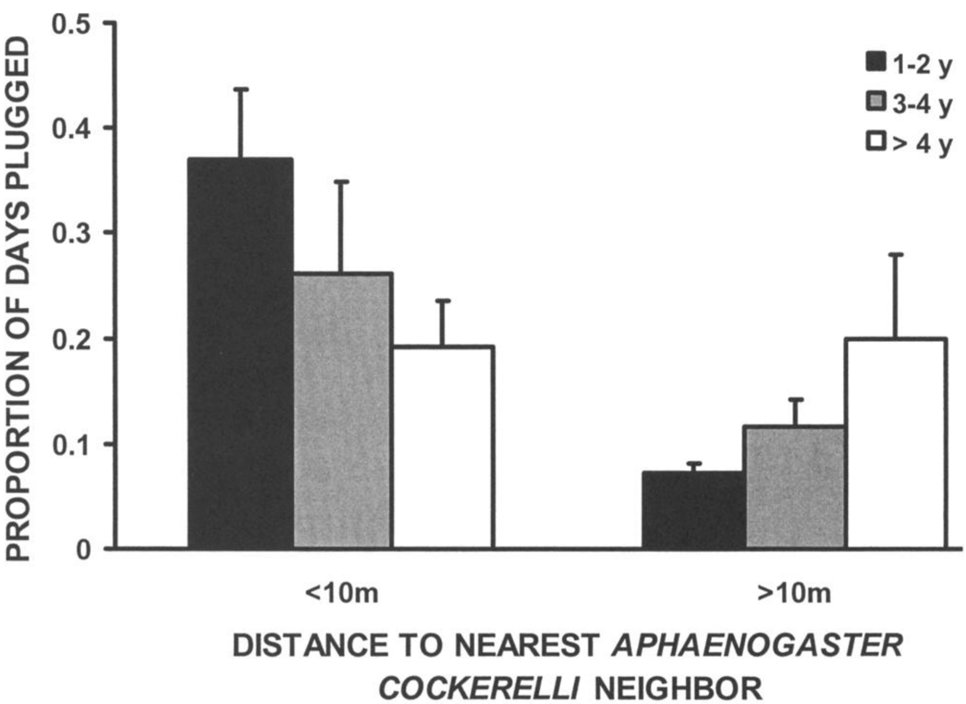

FIG. 1.—The effect of age class and proximity on the probability of being plugged. Bars show the mean (±SE) proportion of days plugged out of all observation days in 1998 and 1999 for colonies plugged on at least 1 d

intensely or encounter most frequently. *Aphaenogaster cockerelli* workers forage up to 35 m from the colony (Hölldobler *et al.*, 1978) and *P. barbatus* foraging ranges extend 40 m from the nest (Gordon, 1991). When foraging ranges overlap, colonies compete for food. The probability of an encounter between two colonies depends on the distance between them (*e.g.*, Gordon and Kulig, 1996).

In another ant species stone-dropping, a behavior similar to nest-plugging, depends on nest proximity. The desert ant *Dorymyrmex* (=*Conomyrma*) *bicolor* drops stones into the entrances of three species of *Myrmecocystus* ants and thereby deters *Myrmecocystus* foraging behavior (Möglich and Alpert, 1979). Möglich and Alpert (1979) found that stone-dropping occurred only when colonies were less than 3 m apart. However, plugging did not depend on proximity alone. *Dorymyrmex bicolor* plugged only active colonies (Möglich and Alpert, 1979).

The probability that a *Pogonomyrmex barbatus* colony was plugged did not depend on proximity to an *Aphaenogaster cockerelli* colony alone; the probability of being plugged declined with distance only for younger colonies.

The effect of *Pogonomyrmex barbatus* colony age on its susceptibility to nest-plugging raises two intriguing questions at the behavioral level. First, why do *P. barbatus* colony age and proximity influence plugging behavior in *Aphaenogaster cockerelli*? Second, once plugging behavior is triggered, how does an *A. cockerelli* colony identify the responsible *P. barbatus* colony from all of its *P. barbatus* neighbors? There are two possible explanations. It may be that *P. barbatus* colonies change the conditions for *A. cockerelli* colonies by reducing resource availability and frequently interfering with workers. When conditions change *A. cockerelli* colonies may respond by adjusting the frequency with which they plug *P. barbatus* colonies. Thus, the effect we see arises because the change in conditions is related to both the age and proximity of *P. barbatus* colonies and to the extent to which *A. cockerelli* respond. Encounter frequency may also influence plugging behavior if younger colonies are not encountered as frequently as distance increases. If the *P. barbatus* colony is small and young, *A. cockerelli* may be able to coexist by plugging the nests of *P. barbatus* colonies. But as the *P. barbatus* colony ages, *A. cockerelli* may be better served by directing its foraging away from the *P. barbatus* colony, thereby reducing the frequency of encounters and competition. Further research is needed to determine both the conditions that elicit nest-plugging behavior and how *A. cockerelli* colonies discriminate among *P. barbatus* neighbors. Future studies aimed at determining the long-term effects of nest-plugging behavior on *P. barbatus* colony fitness and *A. cockerelli* colony persistence can illuminate the relationship between age- and space-dependent behavioral interference interactions and the dynamics of these two populations.

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LITERATURE CITED

ADAMS, E. S. AND W. R. TSCHINKEL. 1995. Spatial dynamics of colony interactions in young populations of the fire ant *Solenopsis invicta*. *Oecologia*, **102**:156–163.

BROWN, J. H. 1998. The desert granivory experiments at Portal, p. 71–95. *In:* W. J. J. Resetarits and J. Bernardo (eds.). Experimental ecology: issues and perspectives. Oxford University Press, New York.

CHEW, R. M. AND J. DE VITA. 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. *J. Arid Environ.*, **3**:75–83.

———. 1987. Population dynamics of colonies of three species of ants in desertified grassland, Southeastern Arizona, 1958–1981. *Am. Mid. Nat.*, **118**:177–188.

DAVIDSON, D. W. 1977. Foraging ecology and community organization in desert seed-eating ants. Ecology, **58**:725–737.

GORDON, D. M. 1984. Species-specific patterns in the social activities of harvester ant colonies (*Pogonomyrmex*). *Ins. Soc.*, **31**(1):74–86.

———. 1988. Nest-plugging: interference competition in desert ants (*Novomessor cockerelli* and *Pogonomyrmex barbatus*). *Oecologia,* **75**:114–118.

———. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *Am. Nat.,* **138**: 379–411.

———. 1992. How colony growth affects forager intrusion in neighboring harvester ant colonies. *Beh. Ecol. Soc.,* **31**:417–427.

———. 1993. The spatial scale of seed collection by harvester ants. *Oecologia,* **95**:479–487.

——— AND A. W. KULIG. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology,* **77**:2393–2409.

———. 1998. The effect of neighbours on the mortality of harvester ant colonies. *J. Anim. Ecol.,* **67**:141–148.

HEINZE, J., S. FOITZIK, A. HIPPERT AND B. HÖLLDOBLER. 1996. Apparent dear-enemy phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi. Ethology,* **102**:510–522.

HÖLLDOBLER, B. 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex. Beh. Ecol. Soc.,* **1**:3–44.

———. 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille). *Beh. Ecol. Soc.,* **3**:19–60.

———. 1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Beh. Ecol. Soc.,* **9**:301–314.

———, R. C. STANTON AND H. MARKL. 1978. Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera) I. Chemical signals. *Beh. Ecol. Soc.,* **4**:163–181.

LANGEN, T. A., F. TRIPET AND P. NONACS. 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. *Beh. Ecol. Soc.,* **48**:285–292.

LEVINGS, S. C. AND J. F. A. TRANIELLO. 1981. Territoriality, nest dispersion, and community structure in ants. *Psyche,* **88**:265–319.

MÖGLICH, H. J. AND G. D. ALPERT. 1979. Stone dropping by *Conomyrma bicolor* (Hymenoptera: Formicidae): a new technique of interference competition. *Beh. Ecol. Soc.,* **6**:105–113.

PACALA, S. W. AND J. A. SILANDER. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. *Am. Nat.,* **125**:385–411.

RYTI, R. T. AND T. J. CASE. 1984. Spatial arrangement and diet overlap between colonies of desert ants. *Oecologia,* **62**:401–404.

———. 1986. Overdispersion of ant colonies: a test of hypotheses. *Oecologia,* **69**:446–453.

———. 1988. Field experiments on desert ants: testing for competition between colonies. *Ecology,* **69**:1993–2003.

SANDERS, N. J. AND D. M. GORDON. 2000. The effects of interspecific interactions on resource use and behavior in a desert ant. *Oecologia,* **125**:436–443.

SIEGISMUND, H. R., V. LOESCHKE AND J. JACOBS. 1990. Intraspecific competition and components of niche width in age structured populations. *Theor. Pop. Biol.,* **37**:291–319.

STAMPS, J. A. AND P. K. EASON. 1989. Relationships between spacing behavior and growth rates: a field study of lizard feeding territories. *Beh. Ecol. Soc.,* **25**:99–107.

THURBER, D. K., M. C. BELL, H. L. BLACK AND C. D. JORGENSEN. 1993. Dispersion and mortality of colonies of the tropical ant *Paraponera clavata. Biotropica,* **25**:215–221.

TILMAN, D. AND P. A. KAREIVA (EDS). 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ.

TSCHUMY, W. O. 1982. Competition between juveniles and adults in age-structured populations. *Theor. Pop. Biol.*, **21**:255–268.

WERNER, E. E. AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.*, **15**:393–425.

WHITFORD, W. G. AND G. ETTERSHANK. 1975. Factors affecting foraging activity in Chihuahuan desert harvester ants. *Env. Ent.*, **4**:689–696.

———, E. DEPREE AND P. JOHNSON. 1980. Foraging ecology of two Chihuahuan desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. *Ins. Soc.*, **27**(2):148–156.

WIERNASZ, D. C. AND B. J. COLE. 1995. Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality and overdispersion. *J. Anim. Ecol.*, **64**:519–527.

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