

Interactions between granivorous and omnivorous ants in a desert grassland: results from a long-term experiment

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Abstract. 1. There is growing evidence that granivorous ants compete for seeds in desert ecosystems. But ants that diverge in diet may still interact strongly if existing colonies deter foundress queens. Granivores (seed eaters) and omnivores (ants that scavenge and feed on plant exudates) are common components of desert ecosystems.

2. The results of a 15-year granivore reduction experiment to explore the responses of two common omnivorous ants, *Forelius cf pruinosus* and *Dorymyrmex insana*, in a desert grassland were analysed. The food competition hypothesis predicts that granivore removal will have no net effect on omnivores. The spatial competition hypothesis predicts compensatory increases in omnivores on granivore removal plots.

3. A grain-based gut poison significantly reduced the densities of three of the four common granivorous ants. Densities of the large-colony (10^5 -worker) omnivore *Forelius* did not increase with granivore removal. In contrast, and consistent with the hypothesis of competition for space, densities of the small-colony omnivore (10^2 – 10^3 worker) *Dorymyrmex* increased on granivore removal plots; however, this effect was only observed in years of high *Dorymyrmex* abundance.

Key words. Ant community, Arizona, competition, desert grassland, omnivore, predation.

Introduction

Long-term experiments provide insights into factors that shape the abundance of co-occurring species (Brown *et al.*, 2001). Such experiments can reveal direct interactions among co-occurring species in the short term and the summed effects of indirect interactions over longer periods (Yodzis, 1988). Ant communities are particularly good subjects for such studies, as ant colonies are relatively sessile and can be counted with quadrats (Agosti *et al.*, 2000). However, few long-term studies of ant communities exist (Kaspari & Majer, 2000).

Ant communities, especially those of deserts, have long been considered structured by competition for food (Davidson, 1985; Hölldobler & Wilson, 1990; Kaspari, 2000).

Food addition experiments often show food limitation (Deslippe & Savolainen, 1994; Kaspari & Valone, 2002; but see Ryti & Case, 1988a; Munger, 1992), and the targeted removal of ant species can result in higher fitness of hypothesised competitors (Davidson, 1985; Ryti & Case, 1988a; Gibb & Hochuli, 2004). But interactions between ant colonies run the gamut from scramble competition for food (Ryti & Case, 1988a) through interference (Gordon, 1988; Holway, 1999) and predation (Mirenda *et al.*, 1980; Franks & Bossert, 1983). For example, many patterns associated with competition for food, like interspecific territoriality (Levings & Traniello, 1981), and the inverse relationship between colony size and colony density (Ryti & Case, 1988b; Adams & Tschinkel, 1995), can arise through predation. In particular, extant colonies often prey upon the periodic rain of newly emerged foundress queens (Hölldobler & Wilson, 1990), effectively eliminating the establishment of colonies near mature nests (Ryti & Case, 1988b). Thus one ant species may increase when individuals of another are removed not just due to competition for

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food, but because, at its earliest life stage, that species is food for other species.

Here, data are summarised from a 15-year study of the dynamics and interactions of a desert ant assemblage in south-western North America. The response of the six most common species, four granivores and two omnivores, was examined to the long-term experimental reduction of the granivores. Species representing both diet strategies are common in productive desert ecosystems (Kaspari, 2000).

Predictions of two hypotheses are contrasted. In the *food competition hypothesis*, the four granivores are assumed to compete more strongly with each other than they do with the omnivores. If true, granivore removal should have little effect on the density of omnivores. The *spatial competition hypothesis* posits that all six species interact by killing each other's foundresses or otherwise compete for nesting space. It predicts a compensatory increase in omnivores on granivore removal plots.

Methods

The study site was located 6.5 km east and 2 km north of Portal, Cochise County, Arizona, U.S.A. (31°55'N, 109°09'W) on an alluvial plain at an elevation of 1330 m. Vegetation at the site consisted of Upper Chihuahuan Desert scrub dominated by shrubs and scattered perennial grasses (Kelt & Valone, 1995). The site contained 24 0.25-ha experimental plots with at least 25 m separating adjacent plots. These were subjected to various experimental treatments (Brown & Munger, 1985). Here, colony densities on six 'Removal' plots treated with AMDRO[®], a delayed gut poison dissolved in oil and soaked into crushed millet, were compared with 14 Control plots that had never been treated with AMDRO[®]. Removal plots were assigned in 1988 and received 1.0 kg of AMDRO[®] once per year in mid-July. Removal plots had previously supported two treatments (seed addition and annual plant reduction) that were discontinued in 1985 and 1987, respectively.

Colonies were censused each year in July after the onset of the summer rains and before summer seed set. Colony abundance was recorded from 49, 2 m radius circles on each plot. The circles were spaced 6.5 m apart in a 7 × 7 array. In each circle, the number of colony entrances was recorded for all species except *Solenopsis xyloni*. Because a *S. xyloni* colony may have many nest entrances, the presence/absence of a *Solenopsis* colony per circle was recorded. For all other species, multiple entrances ≤ 0.5 m apart were assigned to a single colony. To ensure maximal ant activity, censuses were conducted when soil temperatures ranged from 20 to 35 °C, typically in early morning. The census data from three years, 1995–1997, were deleted from this analysis because a different sampling protocol was used.

At the end of each colony census, worker activity at crushed millet baits was monitored. On each plot 25 bait piles (10 cm diameter) were placed in a regular array with at least 9 m spacing between nearest piles. Bait piles were set out at dawn and the number and identity of all ants on each

pile was recorded 1.5 h later. Each year, AMDRO[®] was added to Removal plots after the colony and worker censuses were complete. For all analyses, data from all subsamples within plots were pooled to obtain plot values for each plot each year.

The dynamics of two common omnivore species and four common granivores were contrasted. The two omnivore species, *Forelius cf pruinosus* and *Dorymyrmex insana* (subfamily Dolichoderinae), consume plant exudates and insect corpses and rarely come to seed baits (Creighton, 1950; Holway, 1999). *Forelius*, though one of the two smallest ants, has the largest colonies of the six species with ≈ 10⁵ workers (Kaspari & Valone, 2002). *Dorymyrmex*, in contrast, has relatively large workers, and colonies of 10²–10³ workers (Wheeler & Wheeler, 1986). The four granivores (all subfamily Myrmicinae) include *Pheidole tucsonica* (the numerical dominant) and *Pheidole rugulosa* (Whitford *et al.*, 1981). Both are among the smallest ants and have colonies of 10²–10³ workers (Snelling & George, 1979; S. Cover, pers. comm.). *Pogonomyrmex desertorum* (Cole, 1968) also has colonies of 10²–10³ workers but has the largest workers of the six species. Both *Pheidole* and *Pogonomyrmex* were classified as granivores based on their year-round foraging for seeds and long-term seed caches. *Solenopsis xyloni* is more omnivorous (Trager, 1991) but collects and stores large quantities of seeds in the summer and was *a priori* classified as a granivore (S. Cover, pers. comm.). *Solenopsis xyloni* has workers of intermediate size and the largest colonies of the granivores (10³–10⁴ workers, Snelling & George, 1979).

A repeated measures ANOVA was used to compare the densities of ant species on the six Removal vs. the 14 Control plots. A one-tailed test was performed on the assumption that granivorous ant colonies and worker numbers will be significantly reduced on the Removal plots. A two-tailed test was then used to evaluate the food competition hypothesis (which predicts no change in omnivore densities) and the spatial competition hypothesis (which predicts higher omnivore densities on Removal plots). All statistical tests were conducted using Statistica version 5.1 (Statsoft, 1997).

Results

In 1988, before the poison AMDRO[®] was applied, the number of colonies for all six species did not differ between Removal and Control plots (Table 1, all *P*-values > 0.16). The most abundant species on Control plots were *S. xyloni* and *P. tucsonica*; *D. insana* was half as abundant, and the remaining three species were about 1/10th as abundant.

Patterns of bait use supported the assumption that *Dorymyrmex* and *Forelius* used seeds less than the granivorous species (Table 1). Before the onset of the experiment, Removal and Control plot omnivores averaged 3.5 and 7.4 ants/plot on bait respectively, while granivores averaged 122.5 and 105.1 ants/plot on bait. Furthermore, *Dorymyrmex* and *Forelius* were still least common at bait piles when colony density was factored in. Omnivores averaged 1.7 and

Table 1. Mean (SD) abundance of colonies and workers per plot and results of statistical tests; 1988 pre-treatment data were analysed with ANOVA ($n=6$ pre-Removal plots vs. 14 Control plots) and 1989–2002 data were analysed with repeated measures ANOVA.

	1988			1989–2002			
	Removal Mean (SD)	Control Mean (SD)	<i>P</i> -value	Removal Mean (SD)	Control Mean (SD)	Trt <i>P</i> -value	Time × Trt <i>P</i> -value
Colony abundance							
Omnivores							
<i>Dorymyrmex insana</i>	6.2 (4.0)	9.7 (5.4)	0.17	10.1 (10.1)	6.8 (5.0)	0.07	0.04
<i>Forelius cf pruinosus</i>	1.2 (1.9)	2.2 (4.3)	0.58	2.5 (2.0)	3.7 (2.5)	0.14	0.70
Granivores							
<i>Pheidole rugulosa</i>	4.7 (2.7)	3.7 (4.2)	0.62	3.0 (2.5)	4.6 (2.3)	0.066	0.39
<i>Pheidole tucsonica</i>	24.8 (10.4)	21.8 (11.2)	0.58	8.8 (4.3)	18.7 (8.7)	<0.0001	<0.0001
<i>Pogonomyrmex desertorum</i>	2.2 (3.1)	2.8 (4.2)	0.75	1.5 (1.0)	4.3 (1.5)	0.034	0.88
<i>Solenopsis xyloni</i>	24.5 (11.1)	26.4 (9.6)	0.70	6.7 (3.8)	6.3 (3.5)	0.72	0.35
Worker activity at seed baits							
Omnivores							
<i>Dorymyrmex insana</i>	3.7 (2.7)	8.9 (11.3)	0.29	5.9 (5.1)	3.3 (1.6)	0.11	0.12
<i>Forelius cf pruinosus</i>	3.3 (6.1)	5.9 (11.6)	0.61	0.8 (1.6)	2.3 (2.3)	0.049	0.81
Granivores							
<i>Pheidole rugulosa</i>	35.0 (17.9)	22.6 (24.6)	0.28	3.3 (3.7)	15.1 (12.6)	0.01	0.15
<i>Pheidole tucsonica</i>	190.0 (110.8)	164.8 (158.1)	0.73	21.6 (23.4)	84.2 (65.9)	<0.0001	0.0001
<i>Pogonomyrmex desertorum</i>	32.3 (48.2)	17.8 (46.5)	0.53	1.5 (1.4)	10.9 (11.5)	0.07	0.35
<i>Solenopsis xyloni</i>	231.2 (272.5)	215.2 (232.9)	0.90	85.7 (65.2)	83.3 (64.7)	0.92	0.23

Trt, treatment.

1.8 ants/plot on bait/colony on Removal and Control plots while granivores averaged 9.8 and 7.0 ants/plot on bait/colony.

Following the initiation of the experiment, the number of granivore colonies decreased on Removal plots by about 40% (20 vs. 33.9 colonies/616 m²) as did granivore worker activity (112 vs. 194 workers/plot on bait). However, only three of the four species appeared to contribute to this decrease. The abundance of *P. tucsonica*, *P. rugulosa*, and *P. desertorum* on Removal plots decreased 33–85% relative to Control plots. In contrast, AMDRO[®] had no effect on the abundance of the fourth granivore, *S. xyloni*, the most abundant species at seed baits (Table 1). Similar patterns were seen for the number of workers on bait piles: there was a 4–7-fold reduction in worker numbers for *P. tucsonica*, *P. rugulosa*, and *P. desertorum* on Removal plots compared with Controls, while *S. xyloni* worker numbers did not differ across plot types.

The reduction in granivore abundance and activity was associated with different responses in the two omnivore species. Densities of *Forelius cf pruinosus*, the species with small workers and large colonies, did not change (Table 1); its activity at millet baits, however, significantly declined on Removal plots. In contrast, *D. insana* showed a marginally significant ($P=0.07$) 40% increase in colony and worker abundance on Removal plots that appeared to attenuate with time and/or strengthen only in high population years (Table 1, Fig. 1; time by treatment interaction, $P=0.04$). Thus, the most common omnivore and a common granivore showed a reciprocal response to the granivore Removal treatment, that similarly attenuated over time.

Discussion

The regular application of AMDRO[®] to Removal plots resulted in a significant reduction in the abundance of all granivores except *S. xyloni*. This is despite the poison's ability to reduce populations of the imported fire ant *Solenopsis invicta* (Wilson & Guillaume, 1982), a member of the same subgenus (*Solenopsis saevissima* group). Two other effects of AMDRO[®] on this assemblage are worth noting. First, populations of granivores were not driven to local extinction. This likely reflects the colonisation of our plots by winged foundresses at the outset of the wet season. Foundress queens that escape predation on the soil surface burrow below ground where they produce their first brood (Hölldobler & Wilson, 1990). They thus may never have come in contact with the poison in their first year. Second, *P. tucsonica*, the most abundant species, showed a significant time by treatment interaction ($P < 0.0001$), which is reflected in a decreased abundance on Control plots after 1998 down to the level of the Removal plots (Fig. 1). Since this attenuation of the treatment effect occurred primarily due to changes in Control populations, it seems unlikely that this is the delayed expression of indirect effects (Yodzis, 1988). Instead, this may reflect the result of a multiyear drought at this site. Granivorous ant abundance is limited by summer rainfall in this system (Kaspari & Valone, 2002). During the early years of this experiment (1987–1992) summer rainfall averaged 21.3 cm. In contrast, summer rainfall from 1993 to 2001 averaged only 10.5 cm, which apparently contributed to the approximately 50% decline in the population size of *P. tucsonica* on Control plots from the early to late 1990s (Fig. 1).

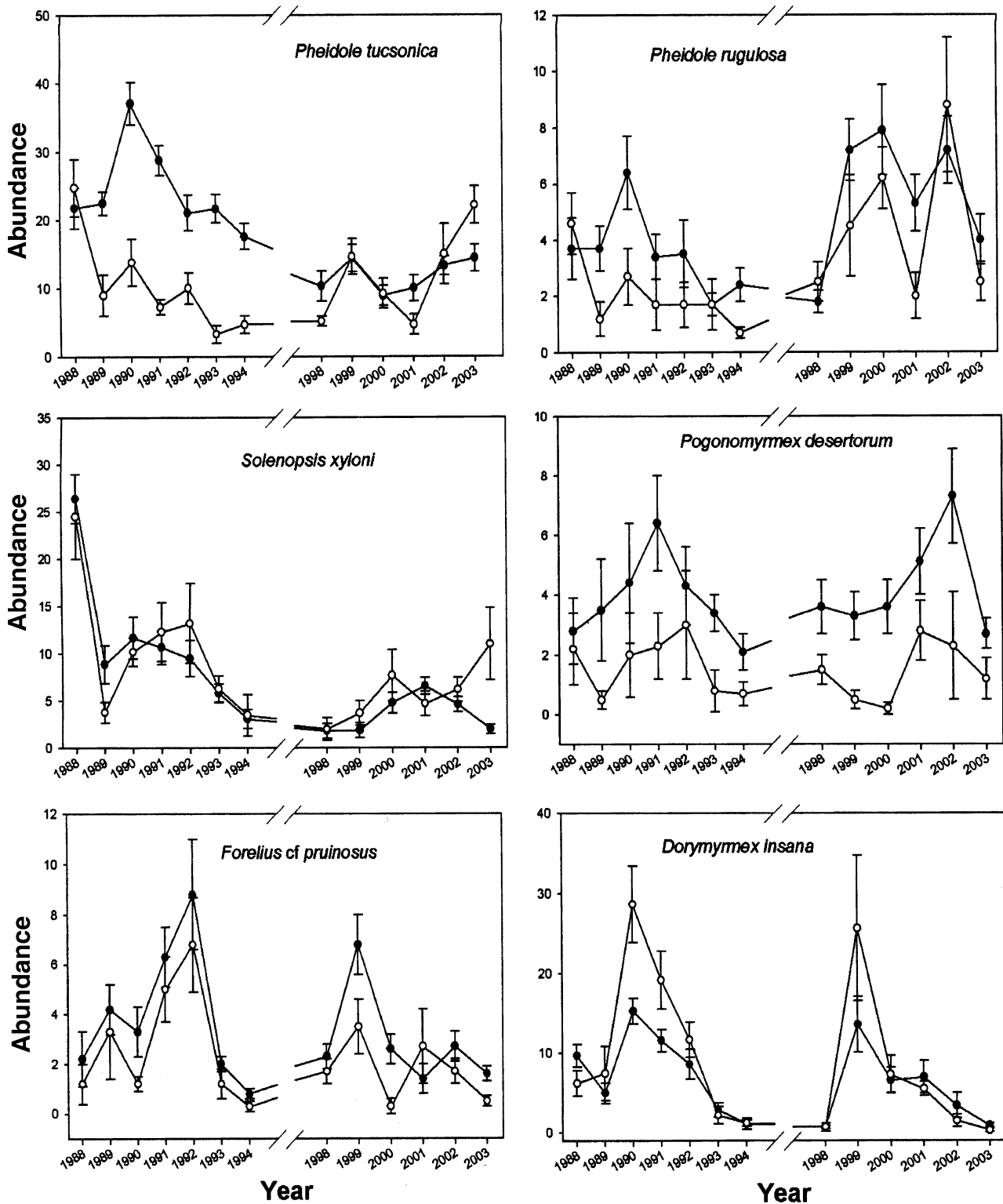


Fig. 1. Mean (±SE) abundance of the six most common species on control (●) and granivore removal plots (○).

The increase in abundance of *D. insana* on Removal plots coincided with a reduction in *Pheidole* and *Pogonomymex* colonies, lending some support to the spatial competition

hypothesis. Two alternate hypotheses are worth considering. One is that omnivores do in fact rely on seeds as a key part of their diet but that seed-eating rodents on Removal

plots consumed the resulting increase in seed availability on Removal plots. This hypothesis is, however, unlikely because it contradicts previous work that found little evidence for competition between granivorous ants and rodents at this site (Valone *et al.*, 1994). Another hypothesis is that granivore reduction resulted in an increase in annual plant biomass that benefited *Dorymyrmex*. This hypothesis, too, can be rejected as previous work has shown that the reduction of granivorous ants does not affect annual plant densities (Samson *et al.*, 1992; Guo & Brown, 1996).

In contrast, *Forelius* with its large colony size (two orders of magnitude larger than *Dorymyrmex*) and low abundance ($\approx 1/6$ th that of *Dorymyrmex*), was less sensitive to changes in the densities of other species. However, the 60% reduction in bait activity by *Forelius* on Removal plots is intriguing, as it is unlikely that this results from direct competition for food. It suggests that *Forelius* may benefit from the activities of *Pheidole* and *Pogonomyrmex* or, alternatively, that *Forelius* colonies suffer from an increase in *Dorymyrmex* populations. While *Dorymyrmex* and *Forelius* have been lumped together as omnivores, recent work by Kay (2002) suggests that species in these genera may differ substantially in diet. Clearly, additional work clarifying the nature of the diets and interactions of the ants in this community is warranted.

In conclusion, the six most common ant species in a desert assemblage displayed a wide variety of responses to a simple perturbation, responses whose strength varied over 15 years. The densities of two common species, *Solenopsis* and *Forelius*, responded neither to AMDRO[®] treatments nor, presumably, to the reductions in *Pheidole* and *Pogonomyrmex* or the increased abundance of *Dorymyrmex* on Removal plots. Gibb and Hochuli (2004) found a similar lack of strong numerical responses among ant genera to the removal of a behaviourally dominant species, *Iridomyrmex purpurpeus*, in an Australian desert. Such data contrast with numerous studies demonstrating strong behavioural interactions between genera and subfamilies (e.g. Holway, 1999; see Hölldobler & Wilson, 1990). This highlights the need, and utility, of removal experiments to further clarify the many mechanisms that may structure ant communities.

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