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Nest-plugging: interference competition in desert ants (*Novomessor cockerelli* and *Pogonomyrmex barbatus*)

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Summary. *Pogonomyrmex barbatus* and *Novomessor cockerelli*, sympatric species of harvester ants in the Lower Sonoran desert, compete for seed resources. This study reports on a method of interference competition. Early in the morning, before *P. barbatus*' activity period, *N. cockerelli* fills the nest entrances of *P. barbatus* with sand. This delays the beginning of the *P. barbatus* activity period for 1–3 h. *P. barbatus* colonies near *N. cockerelli* nests were more likely to be plugged. Nest-plugging shifts the typical daily sequence of *P. barbatus* activities, including the onset of foraging, forward towards midday, when high temperatures force the colony back inside the nest. *P. barbatus* colonies do not compensate for late emergence or events impeding foraging by increasing foraging rate. Thus nest-plugging by *N. cockerelli* decreases the foraging capacity of *P. barbatus* colonies.

Key words: Harvester ants – Interference competition – Lower Sonoran Desert – *Pogonomyrmex* – *Novomessor*

Interspecific competition in ants has been widely studied at the ecological level (e.g. Brian et al. 1966; Davidson 1980; Greenslade 1971; Levins 1973). In many cases, the behavior underlying such competition is not well understood. Recently there has been considerable interest in interference competition between ant species (e.g. DeVita 1979; reviewed in Hölldobler 1983, 1984; Schoener 1983). There are several known examples of interference competition through the use of chemical repellents (Adams and Traniello 1981; Hölldobler 1982), agonistic interactions at territorial boundaries (reviewed in Hölldobler and Lumsden 1980; Levings and Traniello 1981), or food robbing (Hölldobler 1986).

There is one well-known example of interference by mechanical means, which is carried out at the nest entrance of the victim species. *Conomyrma bicolor* drops stones into the nest entrances of three *Myrmecocystus* species (Moglich and Alpert 1979). This deters *Myrmecocystus* foraging, but it is not clear why, because the stones do not fill the nest entrance and stones dropped by investigators had little effect on foraging intensity. Hölldobler (1984) comments briefly on nest-plugging of *Camponotus consobrinus* by *Iridomyrmex pruinosus*, but does not report on the extent or effects of the behavior.

The present paper reports on the most elaborate example discovered to date of interference through mechanical means at the nest entrance. *Novomessor cockerelli* completely fills the nest entrances of *Pogonomyrmex barbatus* with pebbles and dirt, thus temporarily impeding all *P. barbatus* activity outside the nest.

It is clear from other work that *P. barbatus* and *N. cockerelli* are competing for food. Desert harvester ants, including these two species, are part of a complex network of granivorous ant and rodent species that compete for a common food resource, the seeds of desert annuals and perennials (Davidson et al. 1985; Brown et al. 1979). Both *N. cockerelli* and, to a lesser extent, *P. barbatus*, will also take insect food (Hölldobler et al. 1978; Whitford and Ettershank 1975). The two species fight over insect prey, and *N. cockerelli* usually wins, but *P. barbatus* colonies are more effective than *N. cockerelli* ones at retrieving patches of seeds (Hölldobler et al. 1978). The *N. cockerelli* foraging range can extend up to 35 m from the nest entrance; that of *P. barbatus* is about 20 m (Hölldobler et al. 1978; Hölldobler 1976).

N. cockerelli colonies are nocturnal, active from late afternoon until 8–9 a.m., preferring a soil temperature of about 20° C (Whitford and Ettershank 1975). *P. barbatus* is active outside the nest from sunrise at 5 a.m. until about noon (Gordon 1983), preferring a soil temperature of about 40° C (Whitford and Ettershank 1975). The present study was conducted in midsummer, when it is highly unusual for *P. barbatus* to forage at night (Whitford and Ettershank 1975; unpublished work). Ordinarily, then, the two species' foraging periods overlap only for the first few hours of *P. barbatus*' morning activity period.

I here report on observations of nest-plugging by *N. cockerelli*, and examine the following questions: 1) Is nest-plugging more likely in *P. barbatus* nests located near to *N. cockerelli* nests? 2) Does nest-plugging shorten the activity period of *P. barbatus*? 3) Do *P. barbatus* colonies compensate for later emergence, or interference with foraging, by increasing their rate of foraging?

Methods

The study was conducted in a mesquite-chaparral habitat in the Lower Sonoran desert near Rodeo, New Mexico, in July–August, 1985 and 1986.

In some cases, *P. barbatus* colonies plug their own nests. This was sometimes observed during extremely dry periods and may be a method of preserving humidity inside the

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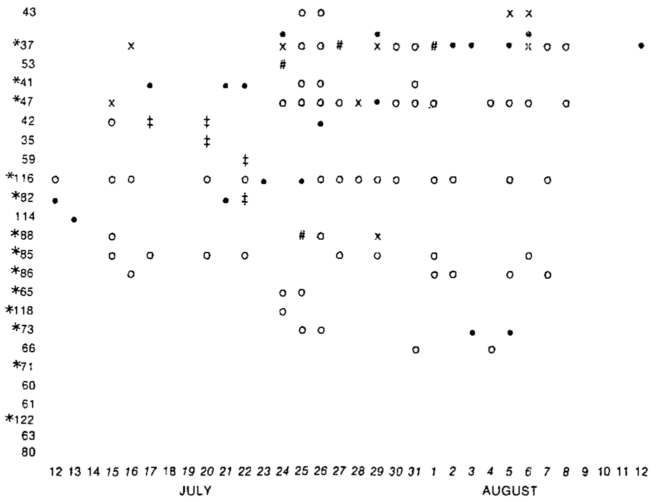
nest. To test whether plugged nests are typically caused by *N. cockerelli* or by *P. barbatus* themselves, whether nest-plugging causes *P. barbatus* to emerge later, and whether the proximity of *N. cockerelli* nests affects the probability of nest plugging, I performed the following experiment for 14 days in July and August 1986. Twenty-four large *P. barbatus* colonies (at least 5 years old (see Gordon 1987)) were selected, divided in two groups: twelve within 15 m of a *N. cockerelli* colony, the other twelve from 15 to 30 m away from one. In 4 days of preliminary observations, *N. cockerelli* were never seen in the vicinity of the latter 12 colonies; they were often seen near the former twelve. In 6 colonies from each group of 12, nest-plugging was prevented by placing plastic collars, consisting of plastic gallon water jugs with the tops and bottoms cut off, around the *P. barbatus* nest entrances. Collars were put down around the nest entrances at about noon, at the end of the daily activity period, and held in place with small rocks, taking care not to shade the nest entrances. In preliminary observations *N. cockerelli* workers were observed to approach the collars, inspect them with antennae and then invariably walk away. In no cases were *N. cockerelli* workers ever found inside the collars, though *P. barbatus* often emerged from the nest and began nest maintenance activities before collars were removed, and occasionally went under and outside the collars.

The following morning after collars were put down, all colonies were checked between 5 and 6 a.m. for nest-plugging and the presence of *N. cockerelli* and collars were removed. The time that the first workers emerged from each *P. barbatus* colony was noted. A 2-way ANOVA was performed on the counts of plugged nests, with proximity to *N. cockerelli* (within 15 m or within 15–30 m) and protection by collars (protected or not) as main effects. Counts of numbers of plugged nests in different treatments were also compared day by day using the Wilcoxon signed-ranks test (Sokal and Rohlf 1969). The time that the first workers emerged from each *P. barbatus* colony was noted.

Harvester ant colonies engage in various activities outside the nest, including foraging; nest maintenance, clearing the nest mound and foraging trails of vegetation, and carrying out sand accumulated during internal nest maintenance activities; midden work, the sorting and upkeep of the colony refuse pile, or midden; and patrolling the nest area and trails for new food sources and disturbances. In *P. barbatus*, nest maintenance, patrolling and midden work are done early in the activity period, while foraging begins later on (Gordon 1983, 1984). A five-year-old colony contains three distinct classes of exterior workers, each of which does either foraging, patrolling and midden work, or nest maintenance (Gordon, unpublished work).

To determine whether colonies that emerge later compensate by increasing their rates of foraging, counts were made each hour of the numbers of foragers within 1.3 m of the nest entrance, on all trunk trails, throughout the morning activity period. Foragers were identified as ants travelling directly toor from the nest on cleared trunk trails as described in Gordon (1984, 1986). Three such daily counts were made for each of 13 large colonies (at least five years old) in the course of 6 days of observation in August 1985, a total of 39 colony-days. These colonies were not disturbed by *N. cockerelli* or any other unusual events.

In all 39 colony-days, all colonies eventually emerged and engaged in the normal sequence of activities, but there was a range of emergence times. I characterized emergence time in terms of the means of two hourly counts of total numbers of ants active from 5–7 a.m. These counts were almost invariably of nest maintenance workers, patrollers, and midden workers, since it was extremely rare for foragers to be active before 7 a.m. The later a colony emerges, the smaller the number of ants already active from 5–7 a.m. This measure of emergence time was used because the first ant to emerge often hovers in the nest entrance for a long time before other activities begin; thus emergence is not an all-or-nothing event that happens at a particular instant. Foraging rate was measured as the total numbers of foragers counted that day in each colony, divided by the numbers of hourly counts made that day. I tested for correlation (Sokal and Rohlf 1969) between number emerged at 5–7 a.m. and foraging rate. Because multiple observations from the same colony could not be considered to be independent, degrees of freedom were calculated as though there was only one observation, rather than three, from each colony ($n = 13$ not 39).



Scheme 1. Observed interference behavior. All *P. barbatus* colonies listed were observed on each of the days shown in italics; not all colonies were observed on some of the remaining days. All observed instances of interference behavior are indicated. Though some colonies were observed at hourly intervals, none of the behaviors shown were counted again when observed more than once for any colony on a given day. * = *P. barbatus* nest within 15 m of *N. cockerelli* nest; ● = *N.c.* piling stones in *P.b.* nest entrance; ○ = *P.b.* nest closed, *N.c.* on *P.b.* nest; # = *P.b.* nest partially closed, *N.c.* on *P.b.* nest; ‡ = *P.b.* nest open, *P.b.* not out, *N.c.* on *P.b.* nest; × = *P.b.* and *N.c.* fighting

Results

Scheme 1 shows all instances of interference behavior recorded in the course of 32 days of observation in July–August 1986. Data for colonies protected by collars are not shown. Nest-plugging (observed on 19 occasions) was done by *N. cockerelli* workers that filled the nest entrances of *P. barbatus* with small pebbles and bits of sand. Nest-plugging was usually done by one or two *N. cockerelli* workers, sometimes with several others standing around nearby. It almost always occurred early in the morning before *P. barbatus* emerged. Occasionally, the nests of small, younger *P. barbatus* colonies (two years old), were plugged by *N. cockerelli* workers after *P. barbatus* workers had already

Table 1. Results of *Novomessor* exclusion experiments. Shown are the total numbers of nests (out of 6) closed at 5–6 a.m. on 14 mornings following the exclusion of *N. cockerelli* by plastic collars

Day	near *Novomessor,* with collars	near *Novomessor,* without collars	not near *Novomessor,* with collars	not near *Novomessor,* without collars
1	3	2	1	0
2	2	4	0	0
3	2	3	1	1
4	0	3	0	0
5	3	3	1	0
6	2	3	0	0
7	2	2	1	0
8	2	2	0	3
9	2	2	1	4
10	1	4	0	2
11	1	3	0	2
12	2	2	1	2
13	3	2	0	1
14	2	2	0	3

begun to emerge. In these cases there was sometimes fighting, but eventually the *P. barbatus* always retreated back into the nest and the *N. cockerelli* went on to close the nest. In all cases of nest-plugging, within 1–3 h the *P. barbatus* workers dug away the material filling their nest entrance and emerged from the nest. In 61 cases, *N. cockerelli* workers were observed circling slowly on plugged nests, probably having just completed nest-plugging. There were 9 instances in which *N. cockerelli* were seen circling on partially plugged or inactive nests. Fighting between the two species, either over food objects or in response to nest-plugging behavior, was observed on 6 occasions. Some colonies were subjected to nest-plugging for many days in succession, the maximum being 6 times for a young colony (colony 37) and 9 times for an older, larger colony (colony 47).

Table 1 shows the results of the collaring experiments. The ANOVA showed significant effects of the presence of collars ($P<0.0025$, $SS=8.64$, $F=10.12$ at 1 df) and proximity to *N. cockerelli* ($P<0.0001$, $SS=28.57$. $F=33.44$ at 1 df), but no significant protection by proximity interaction ($P<0.7736$). A comparison of colonies with and without collars (columns 1 and 3 vs. 2 and 4 in Table 1) showed significantly less nest-plugging in protected colonies ($P<0.01$, Wilcoxon signed-ranks test). Excluding *N. cockerelli* decreases the incidence of nest-plugging activity, showing that *N. cockerelli* activity, and not just *P. barbatus* activity, is responsible for a significant proportion of the closed nests. A comparison of colonies near and not near to *N. cockerelli* nests (columns 1 and 2 vs. columns 3 and 4 in Table 1) showed that *P. barbatus* colonies are subjected to nest-plugging significantly more often when they are near *N. cockerelli* colonies ($P<0.01$, Wilcoxon signed-ranks test).

Colonies with closed nests tend to emerge later. Setting emergence times to 5, 6, 7, 8, or 10, mean emergence time for plugged nests (8.4) was significantly later than for open ones (6.5) (t-test, $P<0.01$). This trend is more marked in closed *P. barbatus* colonies near *N. cockerelli* nests (Fig. 1).

There was a significant positive correlation between number emerged at 5–7 a.m. and foraging rate ($r=0.56$,

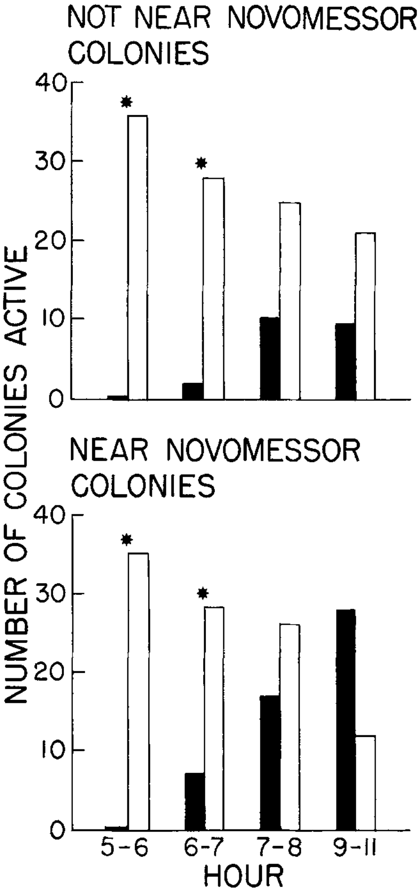


Fig. 1. Emergence time of open and plugged nests, by location. The figure compares the times that colonies plugged at 5–6 a.m. and those open at 5–6 a.m. eventually emerged. Open bars, nests open 5–6 a.m.; filled bars, nests plugged 5–6 a.m. The upper graph shows data for colonies further than 15 m from a *N. cockerelli* nest; the lower for colonies closer than 15 m. $*=P>0.01$, Wilcoxon signed-ranks test

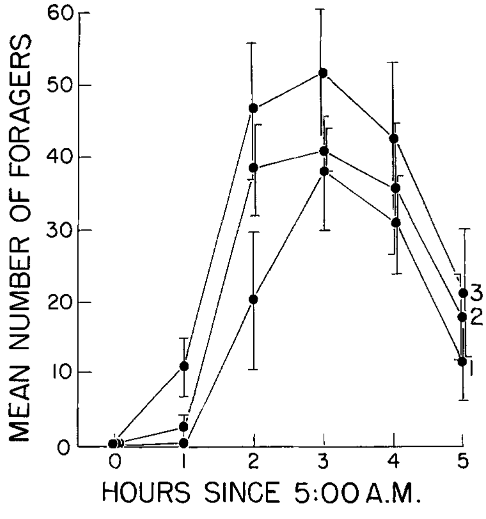


Fig. 2. Activity rhythms of foraging, classified by emergence time. Each point represents mean numbers of ants foraging within 1.3 m of the nest entrance. Data were divided into thirds according to emergence time: 3 = colonies emerging earliest, 3 = intermediate colonies, 1 = colonies emerging latest. Error bars show the standard error of the mean

$P < 0.05$). Figure 2 shows data for the same colony-days plotted as a function of time. Colony-days are divided into three classes (early, intermediate and late) according to mean total numbers of ants emerged at 5–7 a.m. in two hourly counts; shown are the hourly means for each third (each representing 13 colony-days). In both figures, colonies emerging late show a somewhat slower foraging rate than colonies emerging earlier.

Discussion

The activities of a harvester ant colony, foraging, nest maintenance, patrolling, and midden work, are done each day in a characteristic temporal sequence, which I call the "daily round" of the colony (Gordon 1986). Foraging is the last activity in the sequence; it peaks later in the activity period, after nest activities and patrolling have been completed. Except for a final spurt of nest maintenance work, foragers are the last workers active each day and are clearly driven back into the nest by high soil temperatures. On each day that a colony emerges, it carries out the same characteristic sequence of activities (Gordon 1983, 1984).

By forcing *P. barbatus* colonies to emerge later, foraging is pushed later into the activity period. The *P. barbatus* colony that emerges late is left with little time to forage before the afternoon heat forces the colony into the nest until the next morning. One way *P. barbatus* colonies might counteract nest plugging is to increase foraging intensity in the shorter time left available by late emergence. Small sample sizes of plugged colonies within days, and strong differences in foraging intensity between days in undisturbed colonies (Gordon 1984, 1986) make it impossible to design a direct statistical comparison of foraging rate in plugged and open colonies. Instead the question is broken down into the following: Do *P. barbatus* colonies compensate for events impeding foraging by increasing foraging rate? Do *P. barbatus* colonies that emerge later compensate by increasing their foraging rate? Two lines of evidence show that *P. barbatus* colonies do not compensate for interference with foraging.

The first line of evidence is the relation between numbers emerged at 5–7 a.m. and foraging rate, on the same day. If late emergence led to increased foraging rate, the two variables would be negatively correlated. That is, a colony emerging later, with lower numbers already active at 5–7 a.m., would show a higher foraging rate. In fact, colonies emerging late show somewhat slower foraging rates than colonies emerging earlier, and the two variables are positively correlated. Figure 2 suggests the same conclusion: colonies that emerge earlier (i.e. higher numbers of ants emerged early) reach higher foraging rates. While the error bars in Fig. 2 show that this effect is not statistically significant, it is clear that the opposite is not the case. Colonies do not compensate for late emergence by increasing foraging intensity.

Second, in a series of 6 perturbation experiments carried out on 34 colonies in previous years at the same study site, barriers were placed on *P. barbatus* foraging trails to decrease foraging intensity. The colonies did not compensate for the impediment to foraging by increasing the numbers of foragers on the trail. Instead, foraging intensity decreased significantly (Gordon 1986, 1987). Although temporal patterns in various activities may be altered, the sequence of activities is preserved. When foraging is impeded, nest maintenance, patrolling and midden work still precede foraging (Gordon 1986).

Because nest-plugging is more likely near *N. cockerelli* nests, and less likely when *N. cockerelli* is excluded, it is clear that plugged nests can often be attributed to *N. cockerelli* activities. However, *P. barbatus* sometimes plugs up its own nests. The results raise further questions about the function and causes of this behavior.

Since nest-plugging is more likely near *N. cockerelli* nests, it follows that plugged *P. barbatus* nests near *N. cockerelli* nests are more likely to be the result of nest-plugging than are closed nests farther away, which may be the result of *P. barbatus* plugging its own nests. Plugged nests near *N. cockerelli* colonies emerge later than more distant plugged nests (Fig. 1). In *P. barbatus* colonies near *N. cockerelli*, there were 10 plugged and 3 open nests that did not emerge at all on some days (counts are of one colony on one day); in colonies further away, there were 2 plugged and 24 open that did not emerge. These results suggest that colonies plugged by *N. cockerelli* emerge later (or not at all), compared to colonies that plug their own nest entrances.

Within the colonies further from *N. cockerelli*, there were more plugged nests in colonies without collars (Table 1). This effect was not significant (i.e. there was no significant protection × proximity interaction in the ANOVA), but suggests that some colonies without collars were still subject to *N. cockerelli* aggression. In colonies protected by collars, nest-plugging still occurred more often in colonies near *N. cockerelli* nests (Table 1). Perhaps colonies plug their own nests in response to aggression by *N. cockerelli.*

We attempted to mimic nest-plugging ourselves by placing (with forceps) particles of dirt in *P. barbatus* nest entrances early in the morning. This caused excited *P. barbatus* workers to emerge from the nest and remove the obstruction immediately. *N. cockerelli* workers may be using a chemical repellent to prevent *P. barbatus* from impeding their nest-plugging efforts.

Investigations at the ecological level have shown that harvester ant species, including *N. cockerelli* and *P. barbatus*, compete for food. The discovery of nest-plugging behavior sheds new light on how this competition is carried out at the behavioral level. *P. barbatus* exhibits a typical daily sequence of activities, in which the duration of foraging, the last activity in the sequence, is limited by high midday temperatures, and colonies respond to events that impede foraging by allowing foraging intensity to decrease. Because of these dynamics of the *P. barbatus* daily round, colonies that emerge earlier have a better chance of doing more foraging. Thus nest-plugging, which delays the emergence of *P. barbatus*, increases the likelihood that more resources will be left behind by *P. barbatus* to be retrieved later by *N. cockerelli.*

As in most investigations of interference competition in ants, the long-term ecological effects of nest-plugging are not yet clear. It would be interesting to examine what role nest-plugging plays in competition for nest sites, in the survivorship of *P. barbatus* colonies, and in maintenance of the structure of desert ant communities.

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