Distribution of *Myrmecocystus mexicanus* (Hymenoptera: Formicidae): Association with *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae)

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ABSTRACT We examined the spatial pattern of the ant *Myrmecocystus mexicanus* Wesmael. Although intraspecific dispersion is highly uniform, colonies were significantly associated with reproductively mature nests of the harvester ant *Pogonomyrmex occidentalis* (Cresson). Colonies of *M. mexicanus* were more likely to be found within 3 m of *P. occidentalis* and less likely to be found as far as 10 m away. The protein component of the diet of *M. mexicanus* at this site is almost exclusively dead or moribund workers of *P. occidentalis. M. mexicanus* appears to associate with one of its consistent food sources.

KEY WORDS *Myrmecocystus, Pogonomyrmex, Myrmecocystus mexicanus, Pogonomyrmex occidentalis,* spatial pattern, distribution

ONE OF THE most frequently reported patterns in the spatial distribution and ecology of ant species is that colonies are distributed more uniformly than expected in their habitats (Levings and Traniello 1981; Levings and Franks 1982; Ryti and Case 1986, 1992; Hölldobler and Wilson 1990). The most generally accepted explanation for this observation is intraspecific competition for food or space (Ryti and Case 1992), which is hypothesized to be mediated by deaths of queens (Ryti and Case 1988) or young colonies (Adams and Tschinkel 1995a, Wiernasz and Cole 1995) due to intraspecific aggression or exploitation (Hölldobler 1976, Adams and Tschinkel 1995b, Gordon and Kulig 1996). Although the pattern of dispersion among ants is more uniform than expected, it never reaches the perfect uniformity of hexagonal spacing either, because spacing between colonies often depends on the sizes of the colonies involved (Gordon and Kulig 1996, Adams 1998). The deviations from a perfectly uniform distribution may be due to the fact that larger colonies claim larger areas or that colonies of differing sizes differ in their competitive levels. In a highly variable environment, less than perfectly uniform spacing may be due to fluctuations in the intensity of competition.

Much less information is available for the joint spatial distribution of pairs of species. Pairs of species may be either positively or negatively associated with each other or have no detectable association. Species that repel one another include cases of interspecific territoriality (e.g., ant mosaics, Majer 1976a, 1976b; Adams 1994) or checkerboard distributions (Levings and Franks 1982; Cole 1983a, 1983b). Levings and Traniello (1981) predict that under some conditions the multispecies collection itself will be spatially overdispersed, whereas the individual species show random intraspecific dispersion, a pattern observed in some ground-dwelling tropical forest species (Levings and Franks 1982).

Alternatively, species may be positively associated. This includes a tremendous variety of nearly commensal interactions ranging from casual association of nest sites (plesiobiosis) to one species stealing food from another (cleptobiosis) to various forms of parasitic interactions (discussed in Hölldobler and Wilson 1990).

Among desert ants, the pattern of interspecific spacing is variable. Hölldobler (1981) found that *Myrmecocystus mimicus* W. M. Wheeler and *M. depilis* Forel were randomly distributed relative to one another, although each was overdispersed intraspecifically. This finding is similar to that of Bernstein and Gobbel (1979), who examined the spatial distribution of several species of desert ants. In most cases, individual species showed intraspecific regular spacing and there was little evidence for patterns between species. Chew (1987) found that *M. mexicanus, M. depilis,* and *Aphaenogaster cockerelli* (E. André) were overdispersed relative to one another. He interpreted this as the outcome of interspecific competition among these species. Ryti and Case (1984) found that *M. flaviceps* W. M. Wheeler, *Pogonomyrmex californicus* (Buckley), and *Messor pergandei* (Mayr) were all uniformly spaced within a species. However, they found evidence that *Myrmecocystus* was positively associated with both *Pogonomyrmex* and with *Messor.* They interpreted these observations as being a function of the intense intraspecific competition in *Myrmecocystus,* which has uniform intraspecific spacing, forcing col-

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onies into the vicinity of either *Pogonomyrmex* or *Messor.*

Harkness and Isham (1983) and Takacs and Fiksel (1986) report on the joint spatial distribution of *Cataglyphis bicolor* (F.) and *Messor wasmanni* Krausse. They suspected that these two species might show a positive spatial association, because *C. bicolor* was primarily a scavenger on the dead bodies of *M. wasmanni* in Greece. Despite the feeding relationship, they found no evidence for positive association between these two species.

Here, we report on the occurrence of a strong positive association in the spatial distribution of two dominant species of ants, *Pogonomyrmex occidentalis* (Cresson) and *Myrmecocystus mexicanus* Wesmael. We show that *M. mexicanus* is often in close association with colonies of *P. occidentalis* of particular sizes, perhaps because it eats dead or moribund workers of *P. occidentalis.*

Materials and Methods

Pogonomyrmex occidentalis is a widely distributed harvester ant that occurs in western North America in arid grasslands. At our study site in western Colorado we have permanently tagged and mapped a large population (≈1,300 colonies in 29 ha). For details of the study site and the population of *P. occidentalis* see Wiernasz and Cole (1995) and Wiernasz et al. (1995). *Myrmecocystus mexicanus* is sympatric at this location but less common. From 1995 to 1998 we made an intensive effort to find all nests of *M. mexicanus* on the site during our annual censuses for *P. occidentalis.* In the summer of 1997 we permanently marked the location of 108 *M. mexicanus* nests with aluminum tags and mapped their locations with a Leica TC-600 total station (Leica Geosystems, Norcross, GA) from the positions of 10 permanently placed benchmarks (Fig. 1). Previous studies at our site and elsewhere have shown intraspecific overdispersed spatial patterns in either one species (Chew 1987, Wiernasz and Cole 1995) or both species (Bernstein and Gobbel 1979).

The spatial pattern of *M. mexicanus* was tested using a Monte Carlo procedure. The mean and the variance of the nearest neighbor distances of all *M. mexicanus* colonies were determined from their spatial coordinates. Each randomization consisted of 108 points randomly chosen to lie within the study area. The mean and variance in the nearest neighbor distances were calculated for the 108 random points. This procedure was iterated 500 times to estimate the distribution (the mean and the standard deviation) of the mean and variance of the nearest neighbor distance. The deviation of observed mean and variance from the expectations derived from the simulations was expressed in terms of the standard deviations of the randomized distribution and tested with a z-test (Sokal and Rohlf 1995). Because our expectations of a uniform distribution of nests corresponded to an expectation of the mean nearest neighbor greater than expected and the variance in nearest neighbor distances less than expected, we used one-tailed tests.

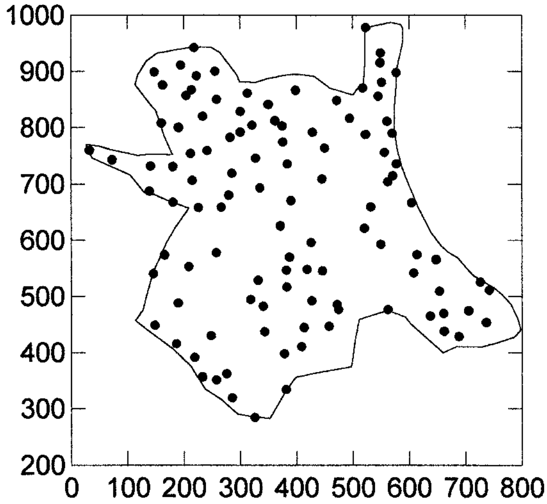

Fig. 1. Positions of 108 colonies of *M. mexicanus* used in this study. Scale is in meters; north is the top of the figure. Outline indicates the boundaries of the study site.

To test for spatial relations between *M. mexicanus* and *P. occidentalis,* a second randomization procedure was performed. Because there is variation in the density of both *M. mexicanus* and *P. occidentalis* within the study area, it was inappropriate to compare nearest neighbor distances of *M. mexicanus* and *P. occidentalis* expectations based on mean density. For each randomization, we selected 1,000 random points to lie within the boundaries of the study site and calculated the distance of these points to the nearest *P. occidentalis* colony. The observed distance of each *Myrmecocystus* colony to the nearest *Pogonomyrmex* colony was calculated directly. These two distributions were then log-transformed (because the distribution of nearest neighbor distances is highly positively skewed) and tested with a *t*-test. To test the association of *M. mexicanus* with *Pogonomyrmex* colonies of particular sizes, we selected *Pogonomyrmex* colonies in size ranges and tested for spatial association in the same manner.

To test for the association of *P. occidentalis* and *M. mexicanus,* while controlling for the effect of the spatial distribution of *M. mexicanus,* we performed another series of randomizations. We randomly placed a *M. mexicanus* to start the simulation and drew a nearest neighbor distance (without replacement) from the distribution of observed *M. mexicanus* nearest neighbor distances. A new colony was located by selecting one of the already placed colonies and placing the new point at the chosen distance in a random direction. The program checked to assure that any newly placed colonies were not nearest neighbors of any other colony and that they were within the plot. All 108 colonies were placed in this fashion and the mean nearest neighbor distances of these points to *P. occidentalis* colonies was computed. This procedure was repeated 121 times. The observed mean nearest neighbor distance to *P. occidentalis* colonies was compared with the distribution of mean nearest neighbor distances from the simulations using a *t*-test of the difference between one observation and an expected distribution (Sokal and Rohlf 1995).

The size of *P. occidentalis* colonies was estimated by measuring the size of the nest cone that is visible above ground. Size was measured as Ln (length NS × length EW × [height +1]), where the measurements are in centimeters. We have shown that this measure is very highly correlated ($r = 0.9$) with estimates of the size of forager force (Wiernasz and Cole 1995). Colony sizes ranged from 4.2 to 13.5. Colonies of approximately size 10 or greater were capable of reproduction (Cole and Wiernasz 2000). Colonies of size 6 or less were very small, usually 1-yr-old colonies, whereas colonies of size 12 or greater were large, mature colonies that will not grow much from year to year. We measured the size of all *P. occidentalis* colonies in 1997. For one size category of *P. occidentalis* colonies, those that were larger than 9.0, we also determined the number of times that *M. mexicanus* colonies were found within particular radii of a *P. occidentalis* colony and tested the difference with a percentage test (Sokal and Rohlf 1995).

In their study of ant communities, Bernstein and Gobbel (1979) used the number of times that one species had another species as a nearest neighbor to examine spatial distributions. If colonies were positively associated, they argued that each should be the others' nearest neighbor more frequently than expected, whereas if they are negatively associated they should be each others' neighbors less frequently. We analyzed our data using this approach as a test of the robustness of our result. We calculated the expected fraction of nearest neighbors of each species from the fraction of the total number of individuals of both species (*P. occidentalis* = 1,349 colonies, 92.6% of the total, *M. mexicanus* 108 colonies, 7.4% of the total). If *M. mexicanus* and *P. occidentalis* were independent of one another, we expected 7.4% of the nearest neighbors of both species to be *M. mexicanus.*

Myrmecocystus mexicanus diet was estimated by observing six colonies over a total period of 23.5 h over 14 d (mainly during early evening 2130–2330 hours and before dawn 0530–0630 hours) during June 1997 and retrieving 145 food items from returning foragers. The colonies used for food were located ≈1 km from the main study site. These *M. mexicanus* colonies averaged 6.9 m from the nearest *P. occidentalis* colony and 34.0 m from the nearest *M. mexicanus* colony. Food samples were collected and identified as possible.

Results

Nests of *M. mexicanus* were more uniformly dispersed than expected by chance (Fig. 1). The nearest neighbor distance between *M. mexicanus* colonies was 35.3 m, whereas the expected nearest neighbor distance was 27.17 m (±1.41 m SD of the expected distribution). The observed nearest neighbor distance was significantly larger than the expectation (*z*-test, $z = 5.02$, $P < 0.001$). The observed variance in nearest neighbor distance was 148.05, whereas the expected variance in nearest neighbor distance was 224.25 (±45.34 = standard deviation). The observed variance in nearest neighbor distances was significantly smaller than the expectation ($z = 1.68$, $P = 0.045$, one-tailed), although only marginally so.

Table 1. Association of *Myrmecocystus mexicanus* colonies to *Pogonomyrmex occidentalis* colonies

Size range of *P. occidentalis* colonies	*t*-value
All colonies	2.30*
4–9	1.61
9–14	2.97***

*, $P < 0.05$; ***, $P < 0.01$.

Myrmecocystus mexicanus were positively associated with *P. occidentalis* (Table 1). Although there was significant positive association with all *P. occidentalis*, it was much stronger for larger colonies. *M. mexicanus* was significantly positively associated with *P. occidentalis* colonies larger than size 9, whereas there was no significant relationship with colonies smaller than size 9. The association of *M. mexicanus* with *P. occidentalis* was produced by a larger fraction of colonies than expected occurring within 3 m of a *P. occidentalis* colony and a significant deficiency of colonies with nearest *P. occidentalis* neighbors at >10 m (Table 2).

Because *M. mexicanus* was not distributed randomly, but was uniformly spaced, it was appropriate to ask whether the apparent association between *M. mexicanus* and *P. occidentalis* disappears when the spatial pattern of *M. mexicanus* is considered. When we forced *M. mexicanus* to have the same distribution of nearest neighbor distances in randomizations as observed, the distance between *M. mexicanus* and *P. occidentalis* was slightly smaller (7.76 m for completely random versus 7.68 m for uniformly spaced *M. mexicanus* that were randomly placed with respect to *P. occidentalis*). However, the conclusion that *M. mexicanus* was positively associated with *P. occidentalis* was unchanged; the distance of *M. mexicanus* to *P. occidentalis* was significantly less than expected ($t = 2.11$, df = 120, $P < 0.025$).

Applying the test of Bernstein and Gobbel, we looked at the identity of nearest neighbors. When *P. occidentalis* and *M. mexicanus* were considered simultaneously, we expected that 7.4% of both the *P. occidentalis* and *M. mexicanus* should have *M. mexicanus*

Table 2. The fraction of *Myrmecocystus mexicanus* colonies that are within a given distance from *Pogonomyrmex occidentalis* colonies that are larger than size 9

Distance interval, m	Fraction of nests within this distance interval		*t*-value
	Expected	Actual	
0–3	0.091	0.167	2.26*
3–5	0.164	0.176	0.32
5–10	0.388	0.463	1.50
>10	0.357	0.194	−3.64***

*, $P < 0.05$; ***, $P < 0.001$.

nearest neighbors. Of the 1,349 nearest neighbors of *P. occidentalis,* 171 were *M. mexicanus,* significantly more than expected (12.7% of the total, $\chi^2 = 54.5, P < 0.001$). All 108 nearest neighbors of *M. mexicanus* were *P. occidentalis* ($\chi^2 = 8.64, P < 0.001$).

Returning *M. mexicanus* workers were primarily retrieving *P. occidentalis* workers. Of the 145 food items retrieved, 112 (77%) of the items were workers of this species. In 15 cases, more than one *P. occidentalis* worker was carried simultaneously. Virtually all the workers retrieved were dead, in only two cases were the workers alive. In one case the living workers were two fighting *Pogonomyrmex* workers. In 10 additional cases, workers of other ant species were retrieved, and in 20 cases other arthropods were retrieved. Approximately 2% of the items retrieved were plant parts.

Discussion

In feeding habits, the *M. mexicanus* at this location seem highly dependent on *P. occidentalis.* Others have noted that *M. mexicanus* often use dead or moribund insects, including *P. occidentalis* (Wheeler 1908, Snelling 1976, Conway 1980). Other species of *Myrmecocystus* are also known to eat *Pogonomyrmex* (Ryti and Case 1984), but they do not appear to specialize (e.g., in *M. mimicus,* termites comprise >80% of the diet, Hölldobler 1981). The extent of specialization on *P. occidentalis* by *M. mexicanus* probably reflects the frequency and abundance of *P. occidentalis* at this location relative to other arthropods. Even though there was significant use of *P. occidentalis,* this use apparently only extends to scavenging rather than extensive predation.

Myrmecocystus mexicanus colonies were extremely uniformly distributed. This is probably a function of the intense territorial conflicts that can occur in species of *Myrmecocystus* (Hölldobler 1976; personal observation). However, within the broad limitations that are imposed by the intraspecific spacing of *M. mexicanus,* their colonies associate with *P. occidentalis.* Although it seems that the uniform spacing of *M. mexicanus* should influence our inference about the association of *M. mexicanus* and *P. occidentalis,* this apparently is not the case. Because *P. occidentalis* is more than 12 times as abundant as *M. mexicanus,* we suspect that even major changes in the distribution of *M. mexicanus* have little effect on the expected spacing between the two species.

Given the apparent specialization on *P. occidentalis* as a source of protein at this site, the association is perhaps not surprising. Because colonies of *P. occidentalis* can persist at a location for 40 yr (Keeler 1993, Wiernasz and Cole 1995), it seems probable that *M. mexicanus* may take the opportunity to move closer to one of their resources. Two instances of colony movement by *M. mexicanus* have occurred during our study. In both, we inferred colony movement by a change in position of the nest entrance of a large *M. mexicanus* colony between annual censuses of our study site. One colony had previously been 5.1 m from a *P. occidentalis* colony when they moved 13.5 m to within 0.2 m of the next nearest *P. occidentalis* colony. A second colony moved from a site 12.3 m from a *P. occidentalis* colony that had died to 6.5 m from an active colony. It is also possible that colony founding may occur preferentially near *P. occidentalis* colonies. Colonies of *P. occidentalis* become reproductively mature at a size of ≈10, therefore *M. mexicanus* associate primarily with colonies that have achieved reproductive maturity. Although they appear to associate with larger colonies, we suspect they are simply moving to areas of higher food density. It seems likely that this is due to the fact that larger *P. occidentalis* colonies represent a larger food resource.

The association of *M. mexicanus* with *P. occidentalis* was not seen in a previous study of the spatial relationships of these ants (Bernstein and Gobbel 1979). One of the very few pairs of species that showed any significant pairwise spatial pattern in that study was *P. occidentalis* and *M. mexicanus,* which were found to be negatively associated in addition to the uniform intraspecific spacing of both species. When we applied the methods of Bernstein and Gobbel (1979) to our data, we found substantial evidence of interspecific attraction. The density of *P. occidentalis* is much lower in the earlier study (15 versus 50 colonies per hectare at a site in northwestern Arizona) and the density of *M. mexicanus* is much higher (20 versus 3.6 colonies per hectare). We hypothesize that the difference in relative density parallels differences in the food availability to *M. mexicanus.* We suspect that the main source of available insect food at our site is *P. occidentalis* and that this is not the case at other, more productive sites.

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