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1974 PROGRESS REPORT
[FINAL]

COMPARATIVE ECOLOGY OF THE HARVESTER ANTS
POGONOMYRMEX BARBATUS (F. SMITH) AND
POGONOMYRMEX RUGOSUS (EMERY)

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ABSTRACT

Factors affecting local geographic distribution, foraging behavior and activity, forage selection, numbers of foragers per colony, nest spacing and nest structure of *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus* were studied. There were seasonal differences in foraging activity. *P. barbatus* was more active in early summer and foraged at night while *P. rugosus* was more active in midsummer, foraging at night during July. Both species exhibited forage preference for grass seeds but took a variety of other materials. Where both species inhabited the same area they had an index of overlap for forage of 0.7. The colonies of both species were randomly distributed. Colony density was approximately 20/ha in areas supporting one or both species. There was no evidence of intraspecific aggression and foraging areas of colonies of the same species overlapped considerably. *P. barbatus* and *P. rugosus* avoid competition by habitat selection. Interspecific aggression probably accounts for the lack of overlap in local distribution.

INTRODUCTION

Harvester ants of the genus *Pogonomyrmex* are common insects in the semiarid regions of North America (Cole 1968). Most ecological studies have concentrated on the western harvester ant, *Pogonomyrmex occidentalis*, which is important in the grasslands of western North America (Rogers 1974, Rogers et al. 1972, Lavigne and Rogers 1974). Few studies have concentrated on the ecology of harvester ants in desert regions (Whitford and Ettershank, in press).

We selected *Pogonomyrmex barbatus* and *Pogonomyrmex rugosus* for intensive study because they are the largest harvester ants in the Chihuahuan Desert (workers 11.8-12.9 mm length and 674 mg and 745 mg live weight, respectively), are closely related (Cole 1968) and it has been suggested that they have similar niche requirements (Hölldobler 1974). We concentrated our studies in an area where both species occur and collected some data for comparison in areas where each species occurs by itself. We studied factors affecting local geographic distribution, foraging activity, forage selection, foraging behavior, numbers of foragers per colony, nest spacing and nest structure.

STUDY AREA

Most studies were conducted at Aguirre Springs, elevation ca. 2000 m, on the east slopes of the Organ Mountains, ca. 40 km east of Las Cruces, New Mexico (Fig. 1). Aguirre Springs is located on several alluvial fans where soil depth varies from a few centimeters to several meters, depending on location with respect to water courses. The soils are sandy loams interspersed with numerous large rock fragments. The vegetation is primarily grassland with scattered trees. Dominant plants are the grama grasses, *Bouteloua gracilis* and *Bouteloua curtipendula*, oak trees, *Quercus* sp., and junipers, *Juniperus* sp. Areas supporting colonies of

P. barbatus and *P. rugosus* are found within a few meters of each other in this area.

Some studies on *P. rugosus* were made on the Jornada Validation Site, ca. 40 km NNE of Las Cruces, New Mexico (Fig. 1). This area is a desert shrub community dominated by mesquite (*Prosopis glandulosa*) and mormon tea (*Ephedra trifurca*) on deep sandy soils with a calcium carbonate deposition layer (caliche) at depths of 0.5-1.5 m below the surface (Schumacher and Whitford 1974). The Jornada site is at an elevation of ca. 1000 m. Perennial grasses are sparse but dense stands of annual grasses and forbs develop during wet periods in the growing season. This area supports five species of *Pogonomyrmex*, but *P. barbatus* is absent.

Some studies on *P. barbatus* were made in two communities on the east slopes of the Chiricahua Mountains near Portal, Arizona (Fig. 1). One area was similar to the Jornada site and the other similar to the Aguirre Springs site at elevations between 1200 m and 1500 m. These areas supported five species of *Pogonomyrmex*, but *P. rugosus* was absent.

LOCAL GEOGRAPHICAL DISTRIBUTION

Collections of *P. rugosus* and *P. barbatus* were made throughout southwestern New Mexico to obtain data on local distributions of the two species. Most areas supported one species or the other, but not both. Cole (1968) showed these two species overlapping completely in the area which was sampled intensively in this study. Our data show that there is a virtual absence of overlap in the local distribution of *P. rugosus* and *P. barbatus* and that, in areas where the two species come together, there are sharp boundaries between them (Fig. 1). Their distribution pattern is not related to soil differences since the same soils support

colonies of each species in different areas (Maker et al. 1974).

There is no consistent relationship between distribution patterns and vegetation since each species inhabits similar plant communities in different areas. Local distribution patterns of these two species can best be understood by comparison of their ecology as presented in the remainder of this paper.

METHODS

NEST DESCRIPTION

Nest descriptions were obtained by careful excavation of colonies. Measurements of chambers were made as uncovered, chamber contents recorded and, where possible, all workers, pupae and larvae were counted. Excavations were abandoned when tunnels to lower layers were lost.

FORAGING ACTIVITY

Foraging activity was recorded by counting numbers of ants returning to a colony per unit time using a reference ring (Schumacher and Whitford 1974). Soil surface

temperatures (T_s) and relative humidity were recorded and activity patterns evaluated with respect to time of day (DSCODE A3UEE10).

NUMBERS OF FORAGERS

Estimates of numbers of foragers per colony were obtained by collecting foragers by aspirators, immobilizing the ants by setting aspirators in a container of ice and marking the immobilized ants. *P. rugosus* were marked by a paint spot on the gaster and *P. barbatus* were marked by removing the terminal segments of an antenna because, unlike *P. rugosus*, they were able to easily remove the paint spots from the gaster. The following day foragers were collected, and marked and unmarked individuals counted. Between 120 and 200 foragers were marked and between 150 and 200 were counted in the census. Numbers of foragers per colony were calculated by the Lincoln Index (Schumacher and Whitford 1974) (A3UEE15).

FORAGE SELECTION

Foragers were collected by aspirator as they returned to the colony with forage material. Between 6 and 12 nests were sampled at two-week intervals. Between 100 and 200 foragers were collected at each nest. The foragers were

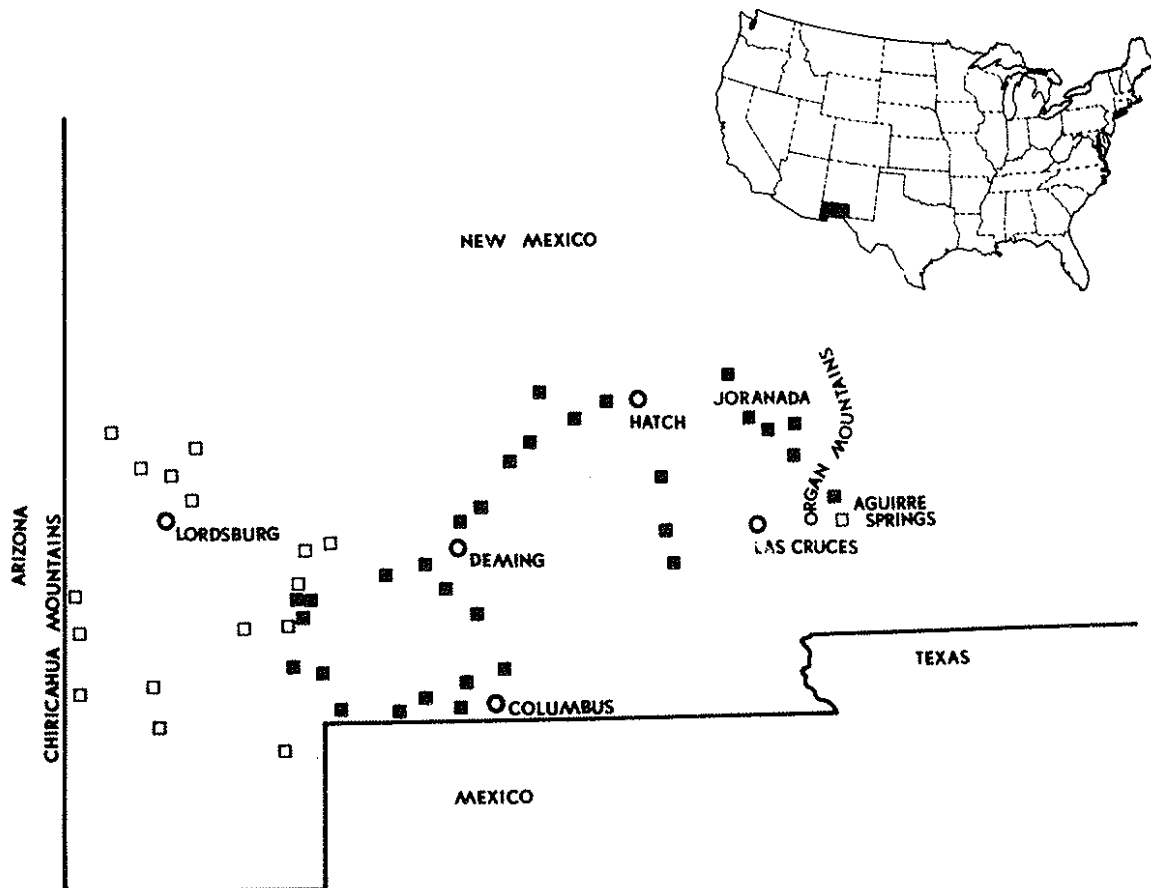


Figure 1. The locations of study sites and local distributions of *Pogonomyrmex rugosus* (solid squares) and *Pogonomyrmex barbatus* (open squares). The map in the upper right shows the study area in relation to the United States.

separated from the materials they had collected and released at the colony. The forage was stored in vials and returned to the laboratory for identification (A3UEE11).

PLANT COVER

Aguirre Springs

Vegetative cover and composition were obtained by line intercept (Phillips 1959). Four 50-m lines were established at 90° intervals around colonies of *P. barbatus* and *P. rugosus*. Grass and forb cover was obtained from six 1-m segments selected at random along the 50 m. Four lines were read at each of six colonies of *P. barbatus* and two colonies of *P. rugosus*.

Portal, Arizona

Density and species composition of annual forbs and grasses were obtained by point-quarter analysis in the desert shrub community (Phillips 1959). Distance measurements were obtained for 80 points and the plants collected. The plants were identified in the laboratory.

Jornada

Density and species composition of plants were estimated by the same techniques as at the Portal, Arizona, area.

COLONY DENSITY AND DISPERSION

Colony densities were estimated by the nearest-neighbor modification of the point-quarter method (Grieg-Smith 1964). Distance measurements from a random point to a colony provide a density estimate and the distance from a colony to the nearest neighbor of the same species provides a measurement used in analyzing dispersion; i.e., PD^2/ND^2 , where PD^2 is the square of the mean distance from the point to colonies of a species and ND^2 is the square of the mean distance from the colony to the nearest neighbor of a species. If PD^2/ND^2 is 1 or nearly 1, dispersion is random; less than 1 indicates clumped distribution; and approximately 0, even distribution (Grieg-Smith 1964, provides charts for determining statistically acceptable levels for various sample sizes).

RESULTS

NESTS

The nests of both species consisted of 12 to 15 broad interconnected galleries radiating out from a central tunnel (Figs. 2 and 3). The surface structures were cleared discs approximately 1 m in diameter with a thin covering of small stones. No nest cones were present. The average height of the galleries was 5 mm (2-8 mm) with diameters ranging from 0.3 to 1.3 m. In *P. rugosus* colonies, only pigmented workers were removed from the galleries in the top 1 m of soil. In *P. barbatus* colonies, callow workers and pupae were taken from the uppermost galleries. In *P. rugosus* colonies, workers, larvae and pupae were taken from the surface galleries. Excavation of four *P. barbatus* nests was terminated when we lost the main tunnel in a very rocky soil layer approximately 0.5 m below the surface (Fig. 3). Excavation of *P. rugosus* nests in winter (January) yielded

few workers in the galleries in the upper 1 m. We terminated excavation when we encountered hardpan caliche at approximately 1.2 m below the surface. Excavation of two of the 10 nests of *P. rugosus* was completed and resulted in recovery of the queen and all workers, pupae and larvae in the colony. All colonies of *P. rugosus* penetrated the hardpan caliche (wet caliche) layer 1.7-1.8 m below the surface (Fig. 2). This layer retained noticeable moisture and was exceptionally difficult to penetrate. In the two colonies completely excavated we found 1595 workers, 2195 workers, 150 larvae and pupae and 180 larvae and pupae.

FORAGING ACTIVITY

Aguirre Springs

P. barbatus and *P. rugosus* exhibited different seasonal foraging activity. In May, *P. barbatus* exhibited greater foraging intensity than *P. rugosus* (Fig. 4). In June, *P. barbatus* exhibited peak activity in late afternoon and continued foraging after sunset. *P. rugosus* exhibited a single peak in the late afternoon. In July, *P. rugosus* had two peaks of foraging activity and foraged after sunset while *P. barbatus* had a single peak in the late afternoon and ceased foraging at sunset.

In May, nearly all colonies of *P. rugosus* were inactive as were some colonies of *P. barbatus* (Fig. 5). In June and July some colonies of both species were inactive under all conditions. *P. barbatus* was active at higher T_S than *P. rugosus*.

Portal, Arizona

In April and May, *P. barbatus* was active in the late afternoon (average number of foragers returning per minute = 8) in the scattered tree-grassland community, but no colonies were active in the desert shrub community. In both plant communities in July, August and early September, *P. barbatus* reached an average peak activity of 30 per minute in the early morning at T_S 20-25 C, dropped to 0 at midday at T_S greater than 35 C, and reached an average peak of 214 per minute between 1600 and 1900 hr at T_S 30-40 C. In spring and late summer there was no nocturnal foraging.

FORAGE SELECTION

Aguirre Springs

The only months in which both species were sufficiently active to provide comparative data on forage selection were June and July. Data on forage were reduced to general classes except for calculating indices of overlap because we recorded over 52 different items of forage. The plant community cover values were: shrubs, 14.9%; forbs, 2.9%; grasses, 39.7%; and trees, 8.1%. In the spring and early summer the only available surface forage was fruits of *Juniperus* spp. and fruits of perennial grasses and some shrubs which probably had recently fallen to the ground. Perennial and annual grasses began to fruit in late July and by late September, mature grass fruits were extremely abundant as were fruits of shrubs, forbs and junipers.

Although fruits of all species were most abundant in September and October, *P. barbatus* exhibited significant preference for the fruits of perennial grasses (Table 1). Termites accounted for 66% of the insect material collected by both species.

We calculated indices of overlap in forage selection by *P. rugosus* and *P. barbatus* by the method described by Horn (1966). In June the index of overlap was 0.73 and in July it was 0.80.

Jornada

In May and June, perennial grass seeds accounted for approximately 50% of the forage collected by *P. rugosus*. As forbs produced fruits in July and August, *P. rugosus* collected these fruits but heavily selected two species of buckwheats, *Eriogonum* spp., which constituted nearly 50% of the forage. These species accounted for less than 20% of the forb species on the site. In September and

October, the two species of *Eriogonum* plus a *Euphorbia* accounted for 70% of the forage collected. During the period when rains stimulated insect activity (July-September) termites accounted for 3% of the forage.

Portal, Arizona

The pattern of forage selection in *P. barbatus* was determined by the habitat. In the scattered tree-grassland habitat, spring forage was 70% fruit parts of *Juniperus* and the sycamore, *Plantanus wrightii*, with the remainder perennial grass seeds and inedible trash. In late summer, perennial grass fruits accounted for 80% of the forage. In the desert shrub community, the fruits of three annual grasses which accounted for 21% of the density of nonwood plants represented 82% of the foraged collected. The annual grasses were: *Aristida adscensionis*, *Bouteloua barbata* and *Bouteloua aristidoides*. Termites represented 2.6% of the forage collected in August and September.

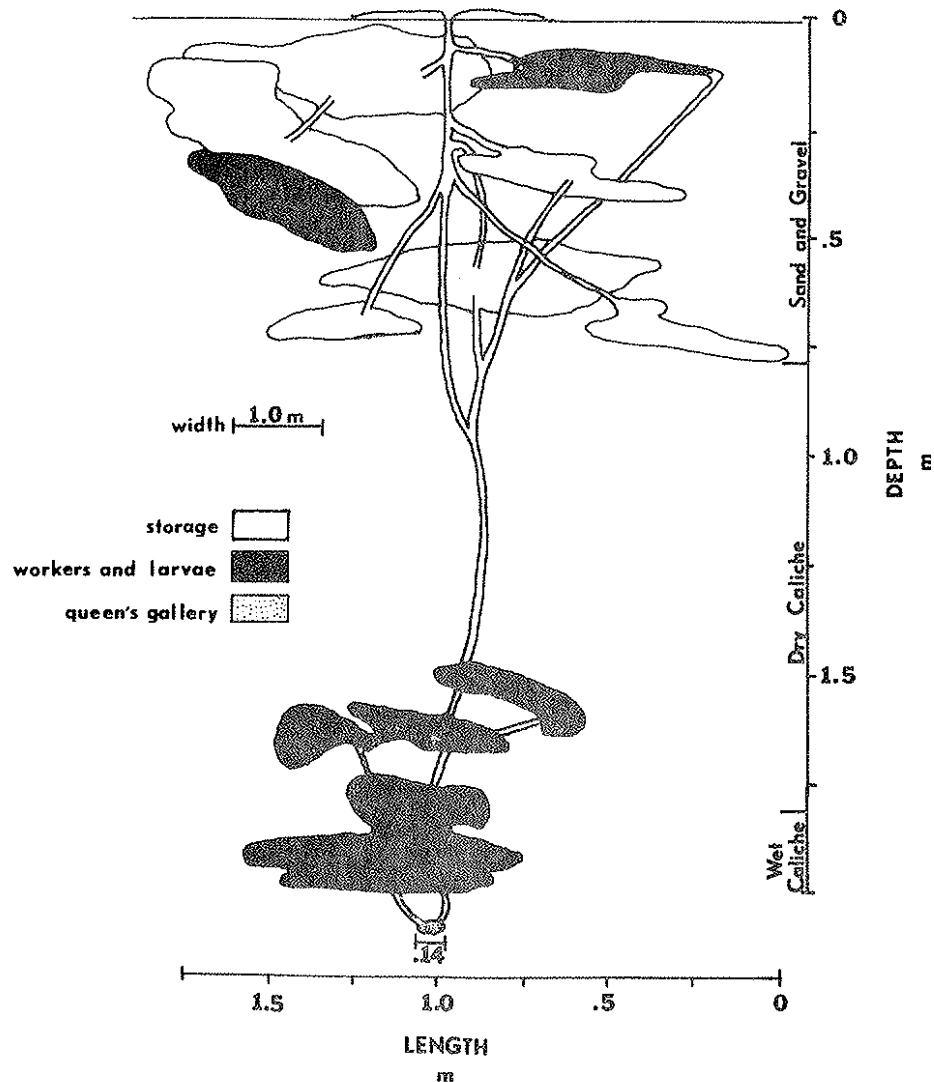


Figure 2. The structure of a nest of *Pogonomyrmex rugosus* excavated at the Jornada site.

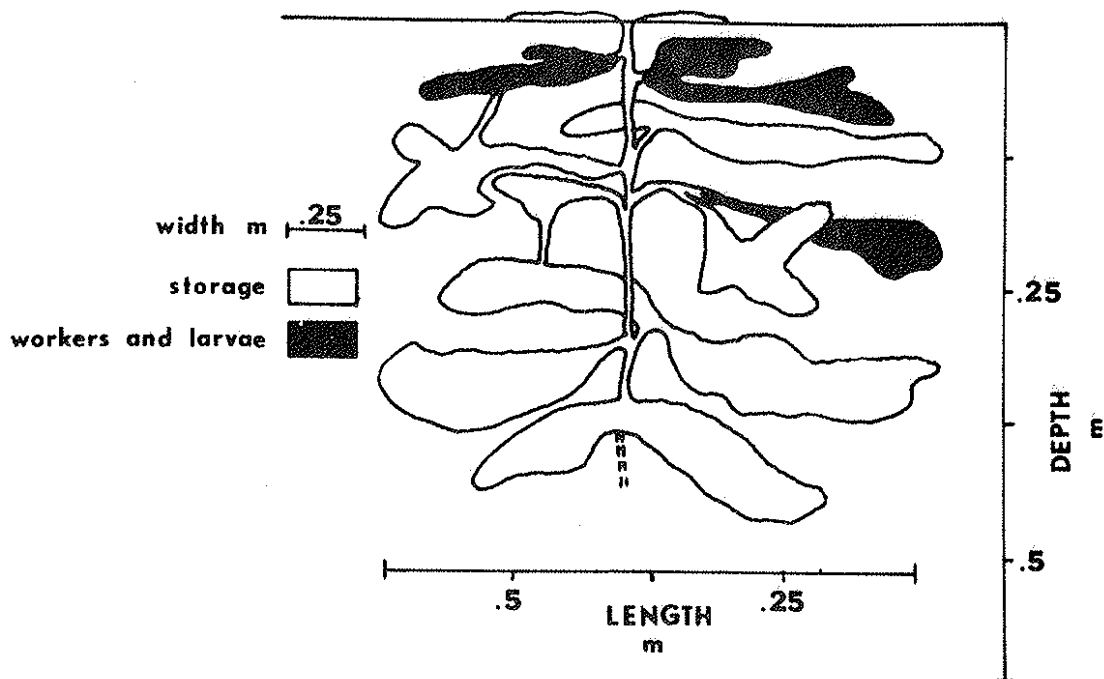


Figure 3. The structure of a nest of *Pogonomyrmex barbatus* excavated at the Aguirre Springs site.

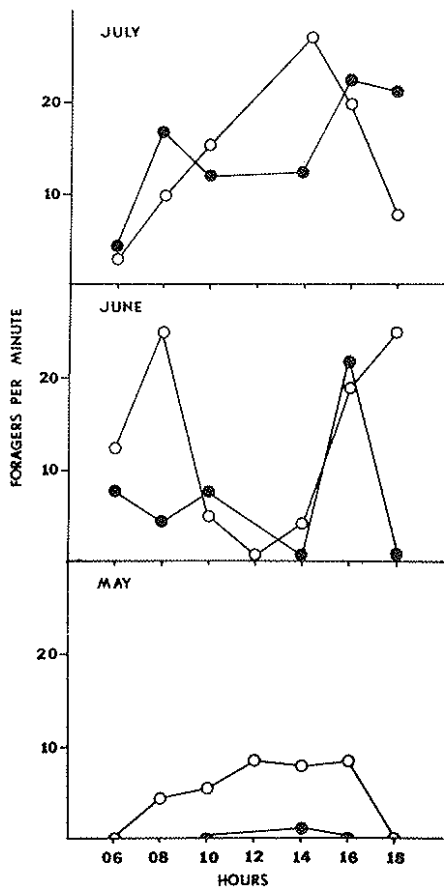


Figure 4. Temporal shifts in foraging activity in *Pogonomyrmex rugosus* (solid symbols) and *Pogonomyrmex barbatus* (open symbols) at Aguirre Springs during May, June and July.

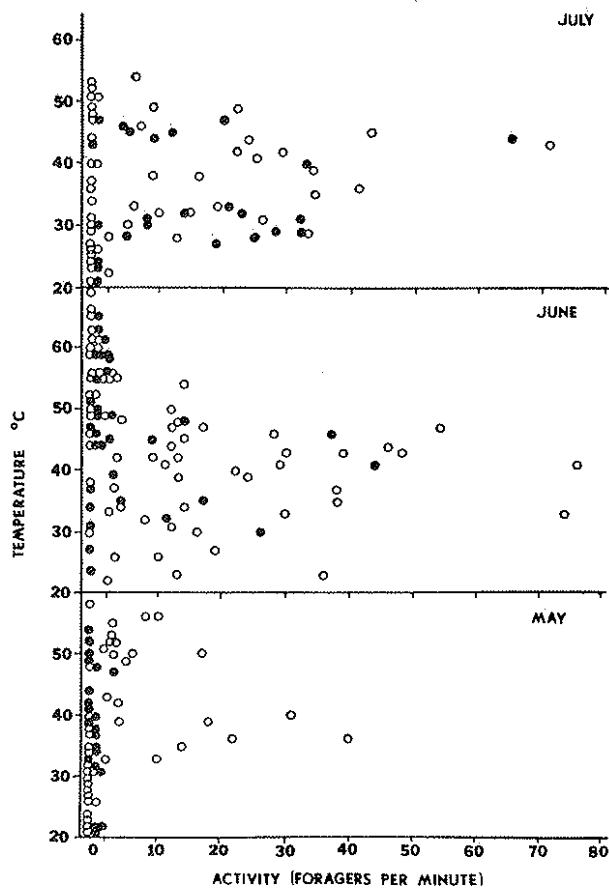


Figure 5. The effect of soil surface temperature on foraging activity in *Pogonomyrmex rugosus* (solid symbols) and *Pogonomyrmex barbatus* (open symbols) at Aguirre Springs during May, June and July.

Table 1. Categories of forage items expressed as percentage of total forage collected by *Pogonomyrmex barbatus* (B) and *Pogonomyrmex rugosus* (R) at Aguirre Springs between May and October 1974. Mean percent cover: shrubs, 14.9%; forbs, 2.9%; grasses 39.7%; trees, 8.1%

	May B	Jun B	Jun R	Jul B	Jul R	Aug B	Sep B	Oct B
Shrub parts	9.0	24.0	11.8	17.4	13.2	25.9	1.2	0
Grasses	63.6	67.4	64.7	36	33.9	43.3	43.6	82.6
Forbs	3.1	1.0	0	3.0	13.2	0	20.2	0
<i>Juniperus</i> sp.	18.1	3.0	0	9.0	7.4	0	0	0
Insects	0	3.0	0	4.2	5.2	5.2	6.5	5.3
Miscellaneous non-edible	6.2	7.6	11.8	30.3	27.2	25.6	28.5	12.3

Table 2. Comparison of numbers of foragers per colony of *P. barbatus* and *P. rugosus* from the different study areas.

Date	<i>P. barbatus</i>	<i>P. rugosus</i>	Site
740701		3289 ± 697	Aguirre Springs
740702		1607 ± 390	Aguirre Springs
740730		2857 ± 710	Aguirre Springs
740731		3392 ± 883	Aguirre Springs
740805	656 ± 58		Aguirre Springs
740805	577 ± 22		Aguirre Springs
740805	271 ± 13		Aguirre Springs
740809	844 ± 80		Aguirre Springs
740809	385 ± 32		Aguirre Springs
740928	1324 ± 194		Portal, Arizona
740928	1809 ± 335		Portal, Arizona
740928	1151 ± 155		Portal, Arizona
740928	1235 ± 177		Portal, Arizona
740928	902 ± 105		Portal, Arizona

NUMBERS OF FORAGERS PER COLONY

There were significantly fewer foragers in *P. barbatus* colonies from Aguirre Springs than in colonies at Portal, Arizona (Table 2). The number of foragers in colonies of *P. barbatus* from Portal, Arizona, were similar to the number of foragers in colonies of *P. rugosus* at Aguirre Springs (Table 2) and the Jornada site (Whitford and Ettershank, in press).

COLONY DENSITY AND DISPERSION

In the area at Aguirre Springs where both species occur, the combined colony density was 22/ha: 15.6 *P. barbatus* and 6.3 *P. rugosus*. Over two-thirds of this area, the minimum distance between colonies of the two species was 46 m. The mean distances ± standard deviation between colonies were 32.1 ± 8.4 m *P. rugosus*-*P. barbatus*; 17.3 ± 7.5 m *P. barbatus*-*P. barbatus*; and 30.93 ± 9.6 m *P. rugosus*-*P. rugosus*. The colony density in an area where only *P. barbatus* occurred was 22.5 colonies/ha. At Portal, Arizona, *P. barbatus* colony density was 20.5/ha

and on the Jornada, *P. rugosus* colony density was 21.3. The dispersion pattern of *P. rugosus* and *P. barbatus* was random ($PD^2/ND^2 \approx 1.21$) at both Aguirre Springs and Jornada.

BEHAVIORAL NOTES

We noted slight differences in the foraging behavior of *P. rugosus* and *P. barbatus*. Although both species utilized foraging trails, *P. rugosus* foragers wandered further from the trunk trails than did *P. barbatus*. On several occasions we observed fighting between *P. rugosus* and *P. barbatus* when *P. rugosus* wandered too close to a *P. barbatus* trunk trail. Where colonies of the two species occurred in close proximity, there was no overlap in foraging area and trunk trails of each species were separate from the other as reported by Hölldobler (1974).

Another incident of interspecific antagonistic behavior was recorded June 13, 1974. A large number of *Myrmecocystus mimicus* annoyed *P. barbatus* on a trunk trail forcing many foragers to drop their booty.

The importance of soil surface temperature in regulating foraging activity of *P. barbatus* was supported by numerous observations at Aguirre Springs and Portal, Arizona. When a human shadow was cast over a colony, workers emerged to forage. When a large shadow was cast by clouds on several occasions, foraging activity was initiated. When the cloud passed, many workers were apparently unable to return to the nest and climbed several centimeters into the vegetation where the ambient temperature was a moderate 35-38 C. On these occasions the soil surface temperature in direct sunlight was greater than 60 C and the shaded soil surface quickly dropped to 40-45 C. *P. rugosus* at Aguirre Springs exhibited similar behavior but this kind of response could not be elicited at the Jornada site.

In July 1973 we performed experiments at the Portal, Arizona, site to compare with similar experiments on *P. rugosus* reported by Whitford (in press). The distribution of foraging effort and degree of overlap in foraging territories of *P. barbatus* were ascertained by clearing a 15-m radius arena around a colony of all surface seeds. We set out seeds (cracked milo), dyed various colors with vegetable dyes, in concentric arcs at 3-m intervals from the central colony. We recorded the numbers and colors of seeds transported to the central colony and four colonies in the periphery of the arena over a 2-hr period for 5 min at 15-min intervals. There was 50-75% overlap in foraging territory of the adjacent colonies with the central colony. On six occasions we observed foragers from an adjacent colony carrying grain across the nest disc of the central colony. We observed no antagonistic behavior between foragers although foragers from as many as three different colonies were collecting seeds from the same place simultaneously. Each colony exhibited a geometric decline in numbers of foragers at a seed source as distance from the colony increased. The distance-foraging intensity relationship fit the expression $\log N = 1.2 - 0.19D$ (Whitford, in press) where N = number of foragers returning per unit time and D = distance in meters.

DISCUSSION

The nests of *P. rugosus* and *P. barbatus* were different from those of *P. badius* (Sudd 1967), but similar to the nests of *P. occidentalis* (Lavigne 1969). The absence of nest cones, fewer galleries and large-diameter galleries were major differences in structure of these nests and the nests of *P. occidentalis*. Lavigne (1969) found seed storage galleries in *P. occidentalis* up to 1.5 m below the surface. In *P. rugosus* nests, storage galleries were confined to the top 1 m.

The penetration of the main nest tunnels of *P. rugosus* into the caliche hardpan attests to the digging ability of this species. The caliche layer was impenetrable by mechanical backhoe and discouraged our digging efforts in almost every case. Galleries in the caliche were perceptibly moister than the more surface galleries. We suggest that the impervious nature of this feature of desert soils acts as an important modifier of the nest environment of desert harvester ants in both summer and winter.

Wilson (1971) states that, as a rule, mature colonies of social insects of the same species are "overdispersed" -- spaced so that distances between them are uniform, not random. "Overdispersion" is to be expected in species which exhibit intraspecific aggression. The distribution of *P. rugosus* and *P. barbatus* was random, which is consistent with the finding that these species do not exhibit intraspecific aggression.

In other harvester ant species that share food and space requirements, competition appears to be avoided primarily by seasonal and daily differences in foraging time (Whitford and Ettershank, in press; Schumacher and Whitford 1974). In areas where *P. barbatus* or *P. rugosus* is the only large harvester ant, there is limited competition with cogeners. However, where the two co-occur, we documented marked differences in seasonal and daily foraging patterns. These foraging patterns were not the same as those in the same species in areas of allopatry (Whitford and Ettershank, in press). Hence, it seems likely that temporal separation is one way in which *P. barbatus* and *P. rugosus* limit the probability of contact and direct aggressive interaction, thereby avoiding competition where they co-occur. Both *P. barbatus* and *P. rugosus* at Aguirre Springs largely avoided competition by nonoverlapping foraging territories and partial temporal separation of foraging time. There is an apparent absence of intraspecific territoriality in these species (Whitford, in press), but interspecific territoriality and conflict were pronounced as shown in this study and by Hölldobler (1974). The local distribution of these species in southwestern New Mexico is consistent with the pattern expected in cogeners with similar niche requirements and which exhibit "contest" competition. Contest competition appears to be largely avoided by habitat selection and in areas of sympatry by avoidance of overlapping territories. Wilson (1971) indicates that territorial fighting among mature colonies of the same and differing species is common and that it has been recorded in *Pogonomyrmex*. However, as indicated previously, we have strong experimental evidence that intraspecific territoriality is relatively unimportant in these species.

Another factor to consider in the local distribution and competition between those species is the numbers of foragers per colony. Numbers of foragers in *P. rugosus* were similar in both areas, but *P. barbatus* at Aguirre Springs had fewer foragers than at Portal, Arizona. It is possible that the Aguirre Spring's habitat is marginal for *P. barbatus*. If, however, we assume that the habitat is marginal for *P. barbatus* and not for *P. rugosus*, then we are unable to explain the success of *P. barbatus* in that area. Also, if frequent "contest" competitive interactions occurred between *P. rugosus* and *P. barbatus*, *P. barbatus* should be at a disadvantage and be dislodged. Since this is a disjunct and small population of *P. barbatus*, the differences in numbers of foragers and some of the behavioral differences may be due to the limited gene pool represented by this small population.

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