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

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**SUMMARY**

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 mid-summer 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 per hectare 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.

**RÉSUMÉ**

**Ecologie comparée des Fourmis récolteuses  
de *Pogonomyrmex barbatus* (F. Smith) et *Pogonomyrmex rugosus* (Emery)**

Nous avons étudié les facteurs qui influencent la dispersion géographique, le comportement et l'intensité de récolte, le choix de la récolte, le nombre d'ouvrières récolteuses dans chaque société, l'intervalle entre les nids ainsi que la structure des nids de *Pogonomyrmex rugosus* et de *Pogonomyrmex barbatus*. Nous avons décelé des variations saisonnières dans le comportement de récolte. *P. barbatus* s'est montrée plus active au début

de l'été et a récolté la nuit, tandis que *P. rugosus* a présenté une pointe d'activité au milieu de l'été, la récolte de nuit se faisant en juillet. Les deux espèces ont manifesté une préférence pour les graines de graminées, mais ont récolté aussi d'autres matériaux. Là où les deux espèces cohabitaient, leur indice d'empiètement pour les récoltes était de 0,7. Les sociétés appartenant aux deux espèces étaient réparties au hasard. La densité des sociétés s'élevait à environ 20 par hectare dans les sites qui abritaient soit l'une soit les deux espèces. Aucune preuve d'agression intraspécifique n'est apparue bien que les territoires de récolte de la même espèce aient été largement imbriqués. *P. barbatus* et *P. rugosus* évitent la concurrence par le choix de l'habitat. L'agression interspécifique explique probablement l'absence d'empiètement des deux espèces dans la distribution locale des colonies.

## INTRODUCTION

Harvester ants of the genus *Pogonomyrmex* are common insects in the semi-arid 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 ETTERS HANK, 1975).

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

Some studies on *Pogonomyrmex 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* (SCHUMACHER and WHITFORD, 1974) on deep sandy soils with a calcium carbonate deposition layer (caliche) at depths of 0.5-1.5 m below the surface. 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.

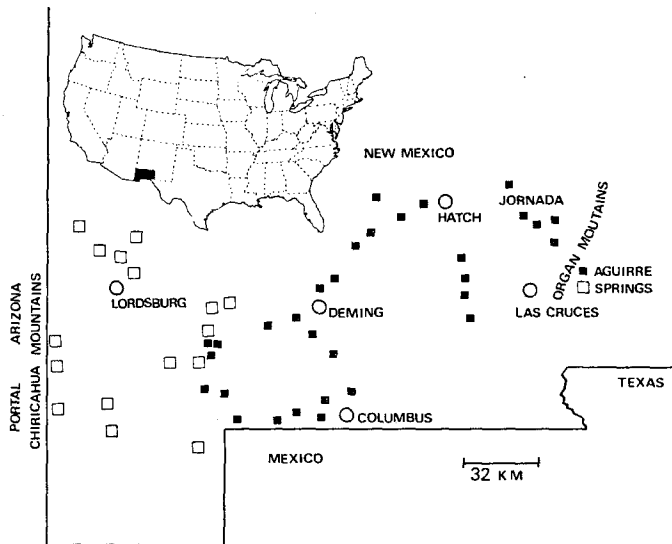


FIG. 1. — The locations of study sites and local distributions of *Pogonomyrmex rugosus* (solid squares) and *Pogonomyrmex barbatus* (open squares). The map in the upper right shows the study area in relation to the United States.

FIG. 1. — Localisation des sites étudiés et emplacements locaux de *Pogonomyrmex rugosus* (carrés noirs) et de *Pogonomyrmex barbatus* (carrés blancs). La carte des Etats-Unis d'Amérique permet de localiser les sites étudiés dans l'état du Nouveau-Mexique.

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 only one species, 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 both species in different areas (MAKER *et al.*, 1974).

We found no relationship between the distribution of these species and vegetation. For example, extensive plant communities of scattered grass clumps of *Hilaria mutica* and *Bouteloua eriopoda* (cover  $\approx 2\%$ ) and scattered mesquite, *Prosopis glandulosa*, and soap tree yucca, *Yucca elata*, occur on the sandy loam soils around Deming and Lordsburg (fig. 1) but only *P. rugosus* inhabits these areas near Deming and only *P. barbatus* inhabits these areas north of Lordsburg. This same pattern is repeated in several plant associations which are common in southwestern New Mexico. 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. At Aguirre Springs, counts were made on six nests of *P. barbatus* and four nests of *P. rugosus* at 1-2 hour intervals during the daylight hours once a week during May, June and July. Activity was checked at night and irregularly during the remainder of the growing season, but counts were not made at regular intervals. At Portal, Arizona, five nests of *P. barbatus* were checked in both areas: the desert shrub area and the grassland-juniper area. Data were collected on 4 consecutive days in April, 2 days in May, 3 days in July, 4 days in August and 2 days in September.

### 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 easily able to 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.

BRIAN (1971) provides a critique of mark-recapture systems for estimating ant populations. The major problems with this method : 1) random dispersal and sampling, 2) durable marks which do not impair activity, 3) suitable sample size, were alleviated because we confined our efforts to estimates of only the foragers in the colonies. This technique provides reliable estimates of the number of active foragers at the time of the estimate but should not be construed to represent an estimate of colony size. Numbers of foragers per colony was calculated by the Lincoln Index (SCHUMACHER and WHITFORD, 1974).

### Forage selection.

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

### Plant cover.

Aguirre Springs : Vegetative cover and composition was 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 lines. 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 was 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 random points to the nearest nest in each quarter of a circle around that point provides

the requisite data for estimating colony density. The distances to the nearest nest of the same species plus the distances to the nests were used to calculate an estimate of dispersion using the mean squared distance of each set of measurements (PIELOU, 1969). If the ratio  $PD^2/ND^2$  is 1, or nearly 1, the dispersion is random,  $>1$  indicates clumped distribution and approximately 0, even distribution.

## RESULTS

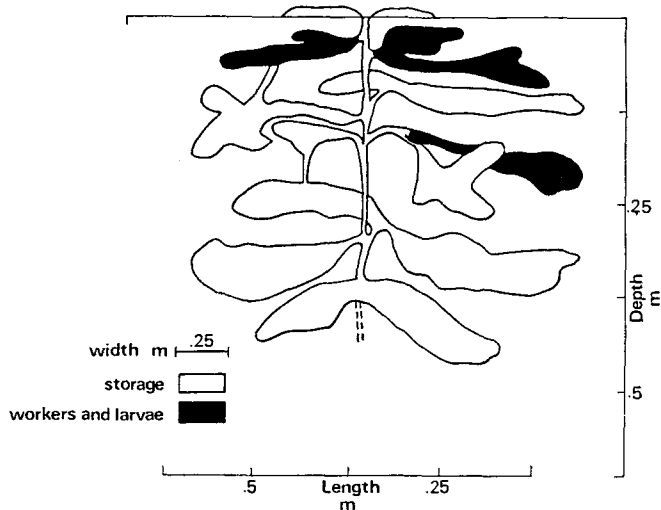
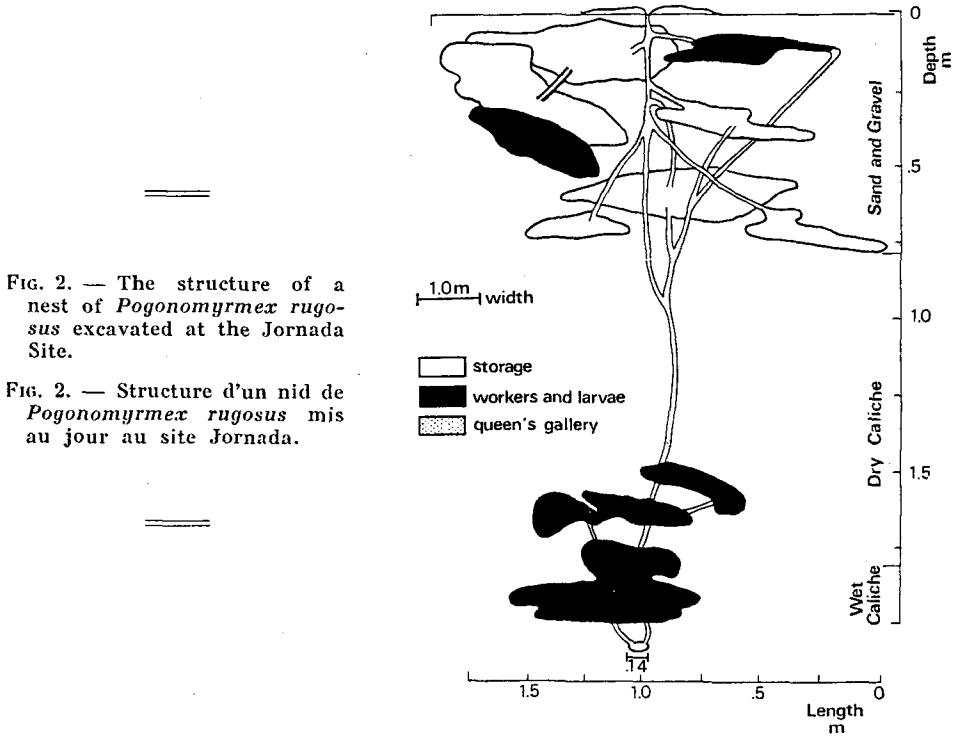
### Nests.

The nests of both species consisted of 12 to 15 broad interconnected galleries radiating out from a central tunnel (fig. 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 hard pan 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*

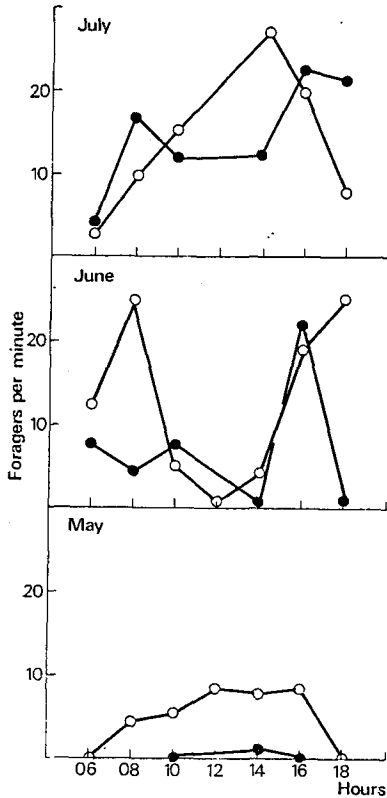


FIG. 4. — Temporal shifts in foraging activity in *Pogonomyrmex rugosus* (solid symbols) and *Pogonomyrmex barbatus* (open symbols) at Aguirre Springs during May, June and July. Data are means for six nests of *P. barbatus* and four nests of *P. rugosus* on five days each month.

FIG. 4. — Variations dans l'intensité de récolte de *Pogonomyrmex rugosus* (cercles noirs) et de *Pogonomyrmex barbatus* (cercles blancs) à Aguirre Springs en mai, en juin et en juillet. Les données représentent les moyennes mensuelles obtenues sur six nids de *P. barbatus* et quatre nids de *P. rugosus* pendant cinq jours.

reached an average peak activity of 30 per minute in the early morning at  $T_s$  20-25 °C, dropped to 0 at mid-day at  $T_s$  greater than 55 °C, and reached an average peak of 214 per minute between 1600 and 1900 hours at  $T_s$  30-40 °C. In spring and late summer there was no nocturnal foraging.

### Forage selection.

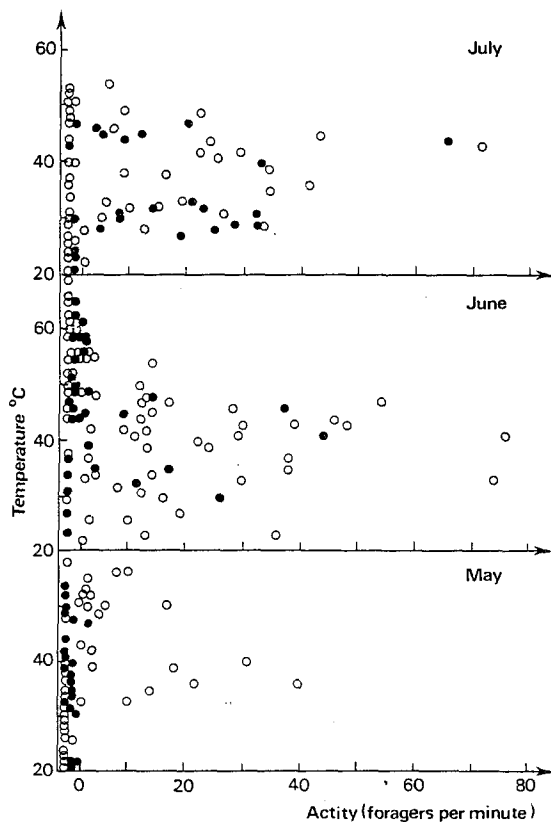
Aguirre Springs : The only months in which both species were sufficiently active to provide comparative data on forage selection were June and July. Data on forage were reduced to general classes except for calculating indices of overlap



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

FIG. 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.

FIG. 5. — L'effet de la température à la surface du sol sur l'intensité de récolte de *Pogonomyrmex rugosus* (cercles noirs) et de *Pogonomyrmex barbatus* (cercles blancs) à Aguirre Springs en mai, juin et juillet.



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 I). 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 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* sp., 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 an *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.

TABLE I. — Categories of forage items expressed as percent 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 %.

TABLEAU I. — Catégories de récoltes exprimées en pourcentages du total des approvisionnements de *Pogonomyrmex barbatus* (B) et de *Pogonomyrmex rugosus* (R) à Aguirre Springs entre mai et octobre 1974. Pourcentages moyens des couvertures végétales : 14,9 % d'arbustes, 2,9 % de mauvaises herbes, 39,7 % de graminées, 8,6 % d'arbres.

	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	36.0	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

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, *Platanus 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 non-wood plants represented 82% of the forage collected. The annual grasses were : *Aristida adscensionis*, *Bouteloua barbata* and *Bouteloua aristoides*. Termites represented 2.6 % of the forage collected in August and September.

### Numbers of foragers per colony.

There were significantly fewer foragers in *P. barbatus* colonies from Aguirre Springs than in colonies at Portal, Arizona (table II). 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 II) and the Jornada Site (WHITFORD and ETTERSHANK, 1975).

TABLE II. — Comparison of numbers of foragers per colony of *P. barbatus* and *P. rugosus* from the different study areas.TABLEAU II. — Comparaison entre le nombre des récolteuses par colonie de *P. barbatus* et celui de *P. rugosus* dans deux des sites étudiés.

Date	<i>P. barbatus</i>	<i>P. rugosus</i>	Site
1974-07-01		3289 ± 697	Aguirre Springs
1974-07-02		1607 ± 390	Aguirre Springs
1974-07-30		2857 ± 710	Aguirre Springs
1974-07-31		3392 ± 883	Aguirre Springs
1974-08-05	656 ± 58		Aguirre Springs
1974-08-05	577 ± 22		Aguirre Springs
1974-08-05	271 ± 13		Aguirre Springs
1974-08-09	844 ± 80		Aguirre Springs
1974-08-09	385 ± 32		Aguirre Springs
1974-09-28	1324 ± 194		Portal, Arizona
1974-09-28	1809 ± 335		Portal, Arizona
1974-09-28	1151 ± 155		Portal, Arizona
1974-09-28	1235 ± 177		Portal, Arizona
1974-09-28	902 ± 105		Portal, Arizona

### Colony density and dispersion.

In the area at Aguirre Springs where both species occur, the combined colony density was 22 per hectare : 15.6 *P. barbatus* and 6.3, *P. rugosus*. In one portion of this area (about 1.5 hectares) colonies of *P. barbatus* and *P. rugosus* were found on a narrow fan between two dry river beds. Colonies of *P. barbatus* were found along one of the stream beds and colonies of *P. rugosus* were aligned along the other. There was no difference in vegetation in this area. The minimum distance between colonies of the two species was 46 m. The maximum distance between *P. rugosus* colonies was 38 m and between *P. barbatus* colonies was 26 m.

In other areas at Aguirre Springs where the colonies of *P. barbatus* and *P. rugosus* were intermixed, the mean distances ± standard deviation between colonies was 32.1 ± 8.4 m *P. rugosus*-*P. barbatus*; 17.3 ± 7.5 m *P. barbatus*-*P. barbatus*; and 30.9 ± 9.6 m *P. rugosus*-*P. rugosus*.

The colony density in an area where only *P. barbatus* occurred was 22.5 colonies per hectare. At Portal, Arizona, *P. barbatus* colony density was 20.5 per hectare 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 the 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 recorded only the occasional contact between the two species as *P. rugosus* wandered too close to a *P. barbatus* trunk trail.

At the Aguirre Springs site, we plotted the distribution of colonies and foraging trails in the area where *P. barbatus* and *P. rugosus* are intermixed. Large trunk trails radiated out from the colonies of both species. Trunk trails of adjacent colonies of *P. barbatus* and *P. rugosus* were interdigitated as described by HÖLLDOBLER (1974) in these species near Portal, Arizona. However, we never recorded overlap in foraging territory that resulted in contact between large numbers of foragers of both species. During the four months of intensive study we recorded only the occasional contact between the two species as reported above.

Another incident of interspecific antagonistic behavior was recorded June 13, 1974. A large number of *Myrmecocystus mimicus* attacked *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 cm 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 (1976). The distribution of foraging effort and degree of overlap in foraging territories of *P. barbatus* was 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 two hour period for five minutes at 15 minute 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  $\log N = 1.2 - 0.19 D$  (WHITFORD, 1976) 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 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 hard pan attests to the digging ability of this species. The caliche layer was impenetrable by mechanical back hoe and discouraged our digging efforts in almost every case. Galleries in the caliche were perceptibly moister than the more superficial 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 both in 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 ETTERS HANK, 1975; SCHUMACHER and WHITFORD, 1974). In areas where either *P. barbatus* or *P. rugosus* is the only large harvester ant, there is limited competition with congeners. However, where the two co-occur, we documented marked differences in seasonal and daily foraging patterns. For example, at Portal, Arizona, *P. barbatus* did not forage at night and in July exhibited peak activity in the afternoon as compared to the Aguirre Springs *P. barbatus* which foraged at night in June and had reduced activity in the late afternoon. *P. rugosus* on the Jornada Site exhibited nocturnal foraging in June and July and two peaks of activity in mid-morning and late afternoon (WHITFORD and ETTERS HANK, 1975) which differs from the pattern of this species at Aguirre Springs. 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 and contributes to the avoidance of competition where they co-occur. Both *P. barbatus* and *P. rugosus* at Aguirre Springs largely avoided competition by non-overlapping foraging territories and partial temporal separation of foraging time. There is an apparent absence of intraspecific territoriality in these species (WHITFORD, 1976), but interspecific territoriality and conflict were pronounced as shown in this study and by HÖLLDOBLER (1974). However, HÖLLDOBLER stimulated intensive conflict involving large numbers of foragers of both species by manipulating the food supply thus changing the loca-

tions of trunk trails so that the trails terminated at the same place. The absence of any major foraging territory overlap during the four months of our intensive study suggests that breakdown of the separation of foraging territories between these two species occurs only rarely and in response to unusual circumstances.

The local distribution of these species in southwestern New Mexico is consistent with the pattern expected in congeners with similar niche requirements and which exhibit « contest » competition. Contest competition appears to be largely avoided because although they use the same habitat types, these habitats are separated geographically. In geographical areas where the two species are intermixed their foraging territories do not overlap. Local distribution patterns of these species probably developed as a result of interspecific « contest » competition. Further understanding of this pattern requires additional study.

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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