Insectes Sociaux, Paris
1984, Volume 31, n° 1, pp. 74-86

SPECIES-SPECIFIC PATTERNS IN THE SOCIAL ACTIVITIES OF HARVESTER ANT COLONIES (*POGONOMYRMEX*)

Deborah M. GORDON

*Department of Zoology, Duke University, Durham, NC 27706, U.S.A.**

Reçu le 19 juillet 1983. Accepté le 19 décembre 1983.

SUMMARY

This field study examines the social behavior of five sympatric species of desert seed-eating ants *(Pogonomyrmex barbatus, P. rugosus, P. maricopa, P. desertorum, P. californicus).* The species differed significantly in measures of activity rhythms in various colony tasks, use of space around the nest yard, and reaction to disturbance. Species differences were related to the typical size of a colony's outside work force. The behavior of *P. rugosus, P. barbatus,* and *P. maricopa,* which had larger outside work forces, emphasized territoriality and the acquisition of food; that of *P. desertorum* and *P. californicus,* which had smaller outside work forces, emphasized the avoidance of contact with other colonies. Examining the patterns in colony behavior can illuminate interspecific relationships in desert ant communities.

RESUME

Différences spécifiques dans le comportement social de cinq espèces de fourmis moissonneuses (Pogonomyrmex)

Cette étude faite sur le terrain dans le désert du sud-ouest des Etats-Unis différencie le comportement social de cinq espèces de fourmis moissonneuses : *Pogonomyrmex barbatus, P. rugosus, P. maricopa, P. desertorum, P. californicus.* Les espèces diffèrent significativement quant à leurs rythmes d'activité pour plusieurs tâches (fourragement, maintien du nid, surveillance, maintien des débris, rassemblement), ainsi que pour l'utilisation de l'espace autour du nid et la réaction de la société à un dérangement. En général, les différences de comportement peuvent s'organiser en fonction de la quantité habituelle d'ouvrières hors du nid. Chez les espèces ayant une plus grande quantité d'ouvrières à l'extérieur du nid, l'organisation de la société met plus en valeur l'acquisition de la nourriture et la territorialité. Par contre, les espèces ayant moins d'ouvrières hors du nid ont un comportement social qui leur permet de réduire leur contact avec d'autres sociétés. En examinant les régularités temporelles et spatiales du comportement social, on peut mieux comprendre les rapports interspécifiques chez les communautés de fourmis.

* Present address : Museum of Comparative Zoology, Harvard University, Cambridge, M A 02138. USA.

INTRODUCTION

Many *Pogonomyrmex* species are parts of desert communities containing other species of the genus. The species are all granivorous and similar in morphology and nest site requirements. Food appears to be a limiting resource (DAVIDSON, 1977 a ; HANSEN, 1978). Behavioral differences among the species are thought to be the result of interspecific competition (WHITFORD and ETTERSHANK, 1975 ; DAVIDSON, 1980). There are suggestions that, in ants, competition leads to selection at the colony level (WILSON, 1971 ; CULVER, 1974), especially selection for differences in foraging strategy (CARROLL and JANZEN, 1973 ; HANZEN, 1978). This study endeavors to find species-specific differences in the colony-level (social) behavior of five sympatric species of desert seed-eating ants *(Pogomyrmex barbatus, P. maricopa, P. desertorum,* and *P. californicus).*

Previous comparisons of the social behavior of *Pogonomyrmex* species have attended almost exclusively to foraging behavior. DAVIDSON (1977 b) compared species that use permanent trunk trails with species that appear to forage randomly, as individuals. Other work shows that aggressive encounters and the spacing of trunk trails play a role in intra- and interspecific competition (HÖLLDOBLER, 1976 a ; HARRISON and GENTRY, 1981). However, some species use trunk trails only part of the time (e. g., on *P. rugosus* : CHEW, 1976 ; BERNSTEIN, 1975 ; DAVIDSON, 1977 a ; HÖLLDOBLER, 1976 a ; RISSING, 1981). Aggressive encounters are reported to be frequent by some authors (DE VITA, 1979 ; HÖLLDOBLER, 1976 a), rare or nonexistent by others (CHEW, 1976 ; WHITFORD *et al.*, 1976). Further examination of colony behavior is needed to characterize foraging strategy, and thereby to understand better the ecology of desert ant communities.

Species-specific differences in the time of day when mating occurs maintain reproductive isolation of the sympatric *Pogonomyrmex* species considered here (HÖLLDOBLER, 1976 b). Except for one study of *P. barbatus* (GORDON, 1983), previous field work on *Pogomyrmex* activity rhythms has examined only overall activity level or mating behavior. The present study investigates species-specific temporal and spatial patterns in a variety of activities around the nest.

METHODS

Field observations were made of 37 colonies in July and August, 1982, in the Chiricahuan Desert, near Rodeo, New Mexico. At one study site, 8 colonies of *P. barbatus*, 5 of *P. desertorum*, and 13 of *P. maricopa* were observed. *P. imberbiculus* workers were seen, very rarely, at this first study site. A second study site contained 5 study colonies of *P. californicus* and 1 of *P. desertorum*. *P. barbatus* foragers occasionally entered the site, but it contained no nests of *Pogonomyrmex* species other than the two mentioned. At the third study site, 5 *P. rugosus* colonies were observed. The nearest nests of other species, *P. maricopa* and *P. desertorum*, were about 30 meters away. All species were active in the morning and inactive during the afternoon. Some species reemerge in the late afternoon. All data were collected during morning activity periods.

Table I. — Classification of colony activities.

Tableau I. — Classification des activités des ouvrières hors du nid.

Foraging	A.	Ants travel directly away from the nest entrance, not carrying anything, on foraging trail if there is one.
	B.	Ants travel directly to the nest entrance carrying a seed or insect bit, on foraging trail if there is one.
Nest maintenance	A.	Carrying out : Ants come out of the nest entrance carrying something, put it down in the nest yard, and go back into the nest.
	B.	Clearing vegetation : Ants climb in vegetation at edge of nest yard, clip pieces of it off with mandibles.
	C.	Ants open nest entrance at the beginning of the activity period by carrying out soil.
	D.	Ants close nest entrance at the end of the activity period by filling it with soil.
Patrolling	A.	Ant walks with frequent stops and changes in direction (compared to foragers). Abdomen is often bent underneath the thorax. Objects and other ants encountered are frequently inspected with antennæ.
	B.	At the site of a disturbance, such as a new object in the nest yard not brought in by ants, ants gather and stand with mandibles open.
Midden work	A.	Ants stand on the midden, repiling it or inspecting it with antennæ.
	B.	Ants move objects from one midden to another midden in nest yard.
	C.	Ants come into the nest yard, not along the foraging trail, bringing small pebbles, and put them down on the nest mound.
Convening		Ants mill around in nest entrance. Frequent antennæ contacts between workers.

In this study, colony behavior outside the nest is divided into five categories : foraging, nest maintenance, patrolling, midden work, and convening, defined in *table I*. In the sequel, foraging will be used only in the sense given in *table I*.

Activity rhythms

Observations were made during the morning activity period to determine whether there exist species-specific rhythms in the five activities. The period was divided into 6 one-hour slots, beginning at 6:00 a.m. Each of the colonies was observed 6 - 20 times, at least once in each time slot, with the exception of the *P. rugosus* colonies, which were not observed during the last time slot. At least one hour elapsed between successive observations of the same colony. An observation was made by recording the number of ants in each of the five previously defined *(table I)* categories of behavior.

Only ants within 1.3 m of the nest entrance were counted. The total number of ants outside the nest but within 1.3 m of it, or observation sum (OS), is the sum of the five numbers (one for each activity). 654 observations were made in 27 days.

The data were analysed using a multivariate analysis of variance (TIMM, 1975). For each colony, the largest OS in any observation was determined. Each observation, consisting of counts of ants in each of the five activities, was converted to 5 fractions of the colony's largest OS, to normalize for differences in colony size. Normalized numbers were then submitted to an arcsin transformation (SOKAL and ROHLF, 1981). For each colony and time slot, the means of the 5 numbers were used as a 5-component vector of responses. The factors considered were species and time slot as main effects, colony nested within species, and species × time-slot interaction, all fixed effects. For each activity, multiple comparisons of species means were made using the Bonferroni test (TIMM, 1975). The test for a species effect employed the colony-within-species effect as its error term.

Reactions to disturbance

To test whether species react differently to the presence of a new object in the nest yard, a small twig about 5 cm was placed on the mound near the nest entrance while the colony was active, away from the trunk trail if one existed. Smaller species were given narrower, lighter twigs. A total of 80 tests were performed on 30 colonies, including some colonies from each species. Each colony was tested at several different times in the morning activity period. The possible effect of colony activities at the time of the test on colony reaction to the twig was not considered in the analysis presented here.

After 6 minutes, colony reaction was scored as: 1) twig was moved somewhere else; 2) twig was inspected but not moved; or 3) twig was inspected and the numbers of ants emerging from the nest decreased sharply. A Fisher exact probability test (SPIEGEL, 1956) was used to determine which species pairs reacted similarly to the twig.

Use of space around the nest yard

To compare uses of space by the five species, a short (2-4 minute) 16 mm film was made showing activities in the nest yards of colonies of each species, during their peaks of foraging activity. Later, with the aid of a stop-motion analysis projector, the paths of some ants were traced and, if possible, their activities identified.

RESULTS

Activity rhythms

Figure 1 shows the temporal patterns of the five activities for each species. *Tables II and III* show the results of the manova. In *table II*, significant values for time slot show that the normalized numbers in each activity depend on the time. That is, the peaks shown in *figure 1* are not results of random fluctuation. Within a species, colonies show different normalized numbers devoted to each task. Only in the case of foraging do colonies of a given species fail to differ significantly.

The normalized numbers of ants engaged in midden work, convening, and foraging are significantly species-dependent. Species differences in the values for nest maintenance are not significant, but close to the 0.05 level. All five species appear to devote similar normalized numbers of ants to patrolling. The significant species x time-slot interaction shows that species

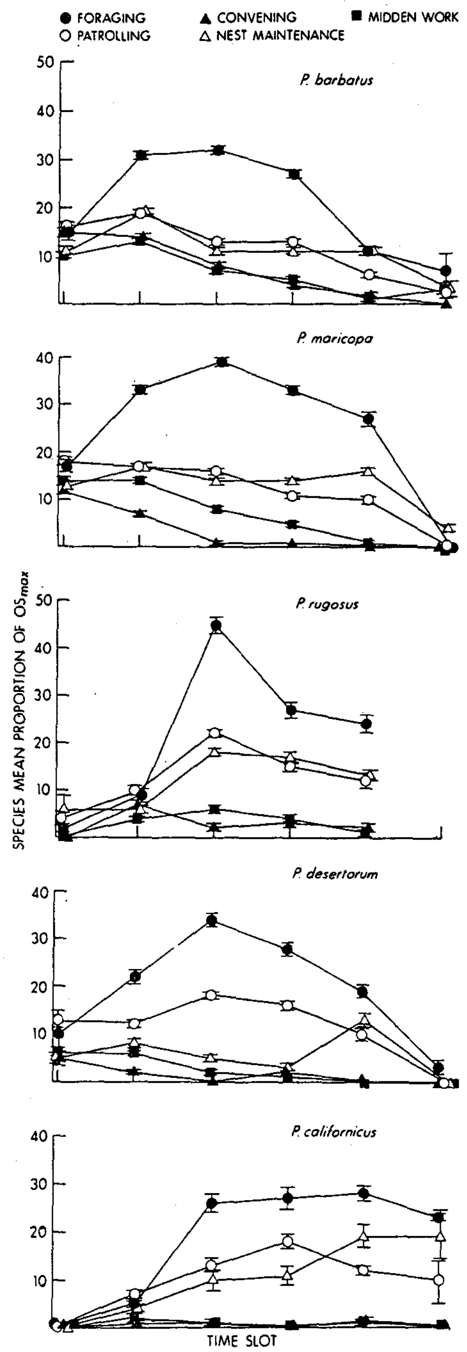

Fig. 1. — Activity rhythms in morning activity period.
For each species, the mean normalized number of the colony's outside work force in each activity is shown throughout the morning activity period. Normalized numbers are shown as percentages. Each line shows the temporal pattern in one of the five activities. The abscissa is hours elapsing since 6:00 a.m. Error bars show the standard error of the mean.

Fig. 1. — Rythmes d'activité pendant la période d'activité matinale.
Pour chaque espèce, la figure montre le nombre normalisé moyen d'ouvrières hors du nid pour chaque activité pendant la période d'activité matinale. Les nombres normalisés sont donnés en pourcentages. Chaque ligne montre l'évolution temporelle d'une des 5 activités. L'abscisse représente les heures depuis 6 h du matin. L'erreur standard est indiquée de part et d'autre de chaque moyenne.

differences in normalized numbers devoted to each activity depend on time, as shown in *figure 2*. One may conclude from *tables II and III* that, although colonies of a given species vary significantly, there are also species-specific activity rhythms that are significantly different from one another.

Table II. — P-values for multivariate analysis of variance.

Tableau II. — Seuils de probabilité obtenus par l'analyse de la variance à plusieurs variables.

Effect	Activity					Manova
	Foraging	Nest maintenance	Patrolling	Midden work	Convening	
Species	0.0420	0.0662	0.8303	0.0028	0.0042	0.01
Colony within species	0.1680	0.0063	0.0119	0.0001	0.0095	0.0001
Time slot	0.0001	0.0029	0.0001	0.0001	0.0001	0.0001
Time slot × species	0.0001	0.0003	0.0001	0.0001	0.0002	0.0001

Table III. — Results of multivariate analysis of variance.
Type III sums of squares *(SS)* and F values *(F)* for all effects, by activity.

Tableau III. — Résultats de l'analyse de la variance à plusieurs variables.
Degrés de liberté *(DF)*, sommes de carrés *(SS)* et coefficient F *(F)*, pour tous les effets, par activité.

		Activity									
		Foraging		Nest maintenance		Patrolling		Midden work		Convening	
Effect	(DF)	SS	F	SS	F	SS	F	SS	F	SS	F
Model	(60)	32695.79	5.39	9949.61	2.61	8673.73	3.16	6222.27	7.26	4603.84	3.87
Error	(142)	14352.07		8825.46		6590.56		2027.60		2812.49	
Species	(4)	1448.99	3.58	1149.46	4.62	119.50	0.65	1158.31	20.28	680.13	8.58
Colony within species	(32)	4131.09	1.28	3752.29	1.89	2605.18	1.78	1824.03	3.99	1153.05	1.82
Time slot	(5)	16037.49	31.74	1188.89	3.83	2327.15	10.18	1117.09	15.65	725.07	7.32
Time slot × species	(19)	8894.45	4.63	3258.42	2.76	3190.18	3.67	1015.65	3.74	1091.38	2.90

In some ways, the five species behave similarly. The peaks in midden work and convening usually occur at the beginning of the activity period ; peaks of nest maintenance occur either at the beginning or at the end of the period ; and foraging peaks in the middle *(fig. 2)*. In general, a colony precedes and follows excursions beyond the nest yard (foraging) with

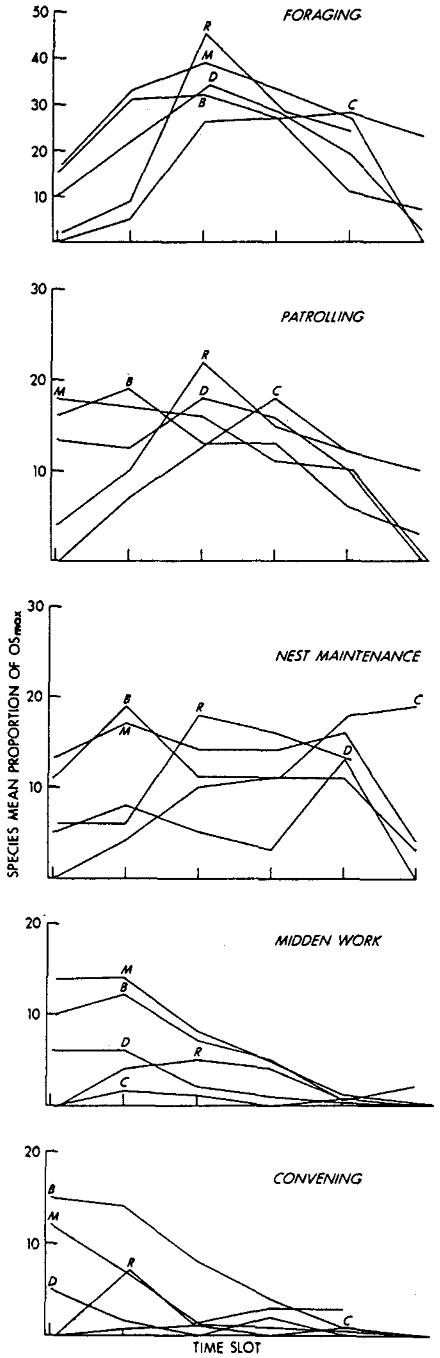

Fig. 2. — Species comparisons of temporal patterns in each activity.
For each activity, the species mean normalized number is shown throughout the morning activity period. Normalized numbers are shown as percentages. Each line represents the activity rhythm of one species. The peak for each species is labelled *(B = barbatus, R = rugosus, M = maricopa, C = californicus, D = desertorum)*. The abscissa is hours elapsing since 6:00 a.m.

Fig. 2. — Comparaisons des espèces pour la répartition temporelle de chaque activité.
Chaque ligne représente les nombres normalisés moyens d'ouvrières obtenus — et dès lors le rythme d'activité observé — pour une espèce et une activité, au cours de la période d'activité matinale. Les nombres normalisés sont donnés en pourcentages. Le maximum d'activité est libellé pour chaque espèce *(B = barbatus, R = rugosus, M = maricopa, C = californicus, D = desertorum)*. L'abscisse représente les heures depuis 6 h du matin.

activities in or near the nest yard (nest maintenance, midden work, patrolling, convening). Each species devotes the largest number of the workers outside the nest to foraging, and the lowest number to midden work and convening.

The results of the Bonferroni comparisons of species means are shown in *table IV*. *Table V* shows the mean and maximum OS for each species. *P. barbatus, P. rugosus,* and *P. maricopa* have the largest numbers of ants outside the nest *(table V)*. These three species devote especially large numbers of workers to foraging *(table IV)*.

Table IV. — Comparison of species mean proportions in each activity.
For each activity, species are listed in decreasing order, top to bottom, of the mean proportion of the colony's outside work force in that activity. Species with the same letter were not significantly different (Bonferroni test, $p > 0.05$).

Tableau IV. — Comparaisons entre espèces des proportions moyennes de chaque activité.
Pour chaque activité, les espèces sont rangées en ordre décroissant, de haut en bas, de la proportion movenne d'ouvrières hors du nid qui font cette activité. Les espèces suivies de la même lettre ne sont pas significativement différentes (test de Bonferroni, $p > 0.05$)

Activity: Foraging		Nest maintenance		Patrolling		Midden work		Convening	
Maricopa	A	Maricopa	A	Rugosus	A	Maricopa	A	Barbatus	A
Barbatus	A B	Rugosus	A B	Maricopa	A	Barbatus	A B	Maricopa	B
Rugosus	A B	Barbatus	A B	Barbatus	A	Rugosus	A B C	Rugosus	B
Desertorum	A B	Californicus	A B	Desertorum	A	Desertorum	B C	Desertorum	B
Californicus	B	Desertorum	B	Californicus	A	Californicus	C	Californicus	B

Table V. — Comparison of species activity levels.
The mean and maximum numbers of ants observed outside the nest within 1.3 m of the nest entrance are shown for each species.

Tableau V. — Comparaison des niveaux d'activité par espèce.
Le tableau montre pour chaque espèce le nombre moyen et le maximum de fourmis hors du nid à moins de 1,3 m de l'entrée du nid.

	Mean	Maximum
P. barbatus	78.22	364
P. rugosus	48.19	162
P. maricopa	41.14	118
P. desertorum	17.80	96
P. californicus	11.38	80

Reactions to disturbance

Table VI shows that *P. barbatus* and *P. rugosus* usually reacted actively to the twig and moved it away. *P. maricopa* and *P. californicus* were likely either to move the twig or ignore it. The reaction of *P. desertorum* was different : colonies would ignore the twig or stop emerging from the nest.

Use of space around the nest yard

Figure 3 shows representative patterns in use of space around the nest yard. The implications of these results are discussed below.

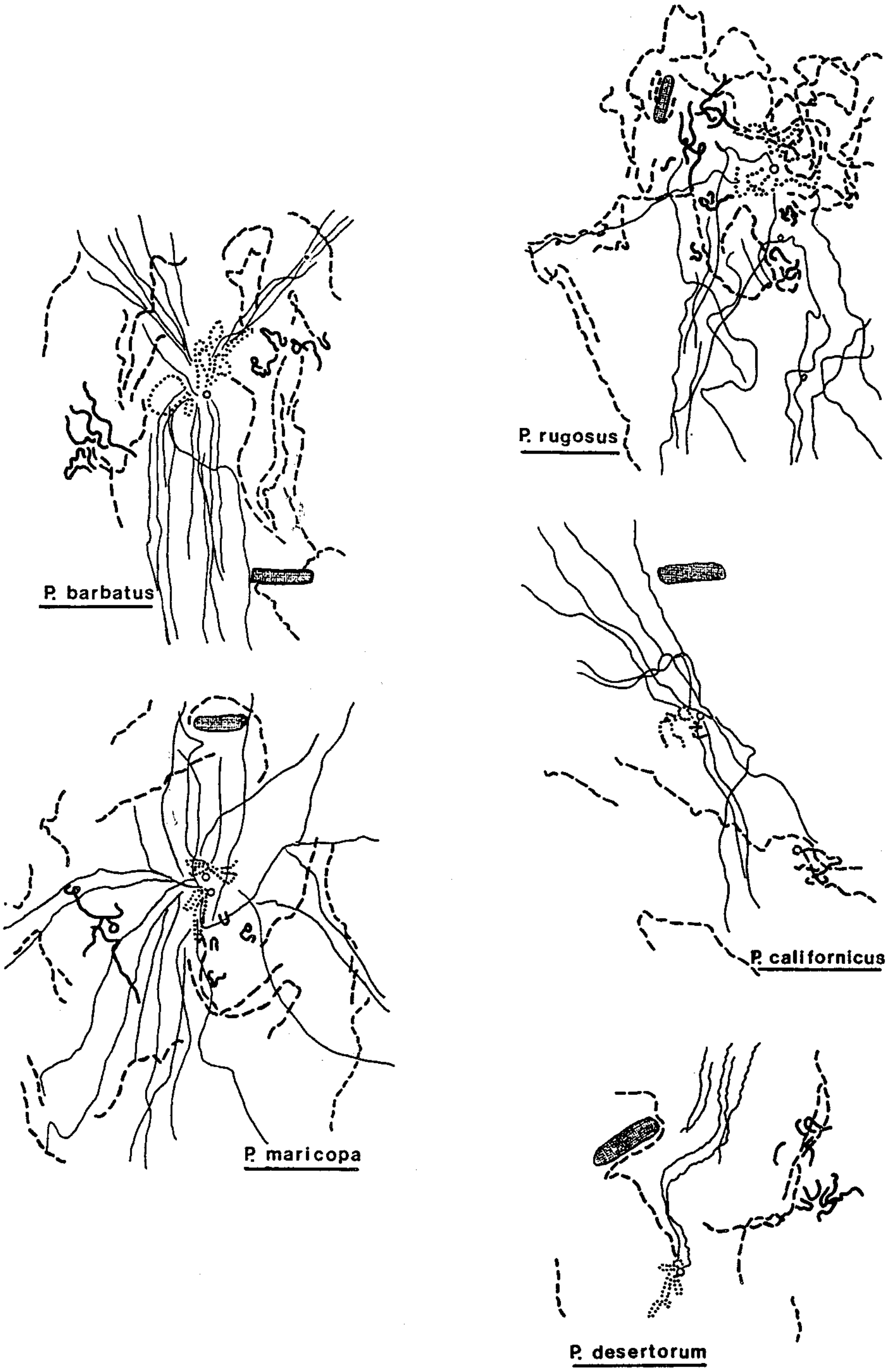
P. barbatus
P. rugosus
P. californicus
P. maricopa
P. desertorum

Table VI. — Comparison by species of reaction to twig placed in nest yard.
The table shows the outcome of all tests. Species with the same letter were not significantly different ($p > 0.05$).
* The difference between *P. rugosus* and *P. maricopa* was almost significant ($p > 0.0584$).

Tableau VI. — Comparaison par espèce des réactions à la brindille placée près de l'entrée du nid.
Le tableau montre les résultats de toutes les expériences. Les espèces suivies de la même lettre ne sont pas significativement différentes (test exact de Fisher, $p > 0.05$).
* La différence entre *P. rugosus* et *P. maricopa* est presque significative ($p > 0.0584$).

	Colony reaction			Results of Fisher's exact test	
	Moved twig	Inspected then ignored twig	Inspected twig, then stopped coming out of nest		
P. barbatus	16	6	0	A	
P. rugosus	8	2	0	A	
P. maricopa	10	12	1	A*	
P. desertorum	3	7	4		B
P. californicus	4	4	0		B

DISCUSSION

When all of the results are considered, each species has unique behavior patterns. However, the five species can be divided into two groups according to typical size of the outside work force. *P. barbatus, P. rugosus,* and *P. maricopa* have a larger outside work force ; *P. desertorum* and *P. californicus*

Fig. 3. — Use of space in the nest yard.
Each figure shows the use of space by workers in and near the nest yard. Figures were derived by tracing the paths of ants visible in a four-minute film of the nest yard. Not all paths are shown. Open circles represent nest entrances ; the shaded area a Swiss Army knife, 8.4 cm long, for scale, or, in the *P. barbatus* figure, a plastic ruler 15 cm long. Paths of foragers are represented by thin solid lines, those of nest maintenance workers by dotted lines, those of patrollers by dashed lines, and those of midden workers by thick solid lines.

Fig. 3. — L'emploi de l'espace autour du nid.
Chaque dessin montre l'emploi de l'espace par les ouvrières autour du nid. Ils furent obtenus en marquant les chemins des fourmis visibles sur un film, de 4 min., des alentours du nid. Tous les chemins existants ne sont pas représentés. Des cercles ouverts représentent les entrées des nids ; l'objet obscur représente un canif, 8,4 cm de longueur, pour montrer l'échelle (remplacé dans le dessin de *P. barbatus* par une règle plastique de 15 cm de long). Les lignes fines et continues représentent les routes des fourrageuses ; les lignes pointillées, celles des fourmis qui assurent le maintien du nid ; les lignes discontinues, celles des fourmis qui surveillent ; et les lignes épaisses et continues, celles des ouvrières s'occupant des débris.

have a smaller one *(table V)*. Several aspects of the behavior of *P. barbatus, P. rugosus* and *P. maricopa* can be interpreted as specializations for more efficient foraging. The three species devote especially large numbers of workers to foraging *(table IV)*. In *P. maricopa* and *P. barbatus*, the peak in patrolling occurs before the peak in foraging. For *P. barbatus*, this sequence was more pronounced the previous year (GORDON, 1983). Since it is patrollers, not foragers, that recruit other ants to food, at least in *P. barbatus* (GORDON, 1983), the activity sequence may allow more foragers to be recruited to new food sources. The use of trunk trails, especially consistent in *P. barbatus*, may help the colony to harvest rich food sources more quickly (DAVIDSON, 1977 b). *Figure 3* shows that even when *P. maricopa* does not use trunk trails, foragers effectively cover the area around the nest.

The behavior patterns of these three species seem to emphasize territoriality. It has been suggested that *Pogonomyrmex* species defend their nest yards more actively than they do the rest of the foraging ranges (HARRISON and GENTRY, 1981 ; HÖLLDOBLER, 1976 a). Patrollers of both *P. maricopa* and *P. barbatus* had nearly covered the perimeters of the nest yards during the few minutes of filming *(fig. 3)*. Both *P. rugosus* and *P. barbatus* reacted actively to the placement of twigs in the nest yards, as did *P. maricopa* to a lesser extent.

The behavior patterns of *P. rugosus* are unusual. Peaks in patrolling, foraging and nest maintenance all occur simultaneously *(fig. 1)*. The activities of midden workers and nest maintenance workers carrying sand out of the nest are not spatially segregated in the nest yards, as they are in other species *(fig. 3)*. *P. rugosus* is known to vary greatly in the times it is active and in the types of forage it takes, depending on seasonal variations in food abundance (WHITFORD, 1978). Such flexibility may require a specialized patrolling system. Foragers in *P. rugosus* make more frequent turns than do those of other species *(fig. 3)*, apparently covering more ground. Even when using trunk trails, *P. rugosus* seems ready to switch to an individual foraging strategy. Also, the nest yards are patrolled more exhaustively than those of the other species *(fig. 3)*. Thus *P. rugosus* seems to use an all or none approach to locate and harvest food, and to maintain the territorial integrity of the nest yard.

In contrast to the three species discussed above, the behavior patterns of *P. desertorum* and *P. californicus* seem to be specialized for avoiding contact with non-members of the colony, rather than for the acquisition of food and territoriality. They have the smallest numbers of foraging workers *(table IV)*. The perimeters of their nest yards are not covered as frequently by patrollers as in the other three species *(fig. 3)*. Their peaks of nest maintenance come at the ends of the activity periods, in a sequence that may help the colony to avoid encounters with other ant species, already foraging when *P. californicus* and *P. desertorum* are just beginning to be active.

In *P. desertorum*, a twig placed on the nest mound was sometimes enough to cause a decrease in the numbers of workers emerging from the nest *(table VI)*. DAVIDSON's (1980) report, that food items taken by *P. desertorum* varied so as to avoid the seeds preferred by *P. rugosus*, supports the characterization of *P. desertorum* as a timid, behaviorally subordinate species.

The entire activity period of *P. californicus* is later than that of other species *(fig. 1)*, which tends to diminish its contact with other species. Unlike the other species, it keeps its midden inside the nest (DE VITA, 1979; RISSING, 1981), reducing the number of workers needed outside the nest. (However, a few midden workers were seen piling seed husks outside the nests). Furthermore, its colonies relocate frequently, apparently to avoid being too close to other colonies (DE VITA, 1979).

In general, foraging strategy and territorial behavior are elements of the colony behavior patterns described here. The numbers a colony devotes to foraging, the time when workers forage, the sequence in which patrolling and foraging occur, the spatial arrangement of foragers– all are aspects of foraging strategy. Territorial behavior includes the timing and location of exposure to contacts with non-members of the colony, the timing of excursions into the home range of other colonies, and the extent to which the nest yards are patrolled and defended. To investigate how contact between species is mediated, and how food resources are partitioned, it is useful first to understand the patterns of colony behavior.

If we understood completely the spatial and temporal regularities in the behavior of *Pogonomyrmex* colonies, we could predict interspecific relationships. Such a full understanding has not yet been achieved. For example, the variation with habitat of species-specific behavior will need to be investigated. Characterizing species by colony behavior patterns can illuminate interspecific relationships in desert ant communities.

ACKNOWLEDGMENTS. — The study was done at the Southwestern Research Station in Portal, Arizona, and was supported by a grant from the Theodore Roosevelt Memorial Fund. I thank Mr and Mrs Finn RICHARDS for allowing me to use their land as a study site. K. ROTH and B. BAILEY provided invaluable assistance in the field, and discussions with G. ALPERT, R. CHEW, B. HÖLLDOBLER and D. DAVIDSON were very helpful. The Insect Identification Institute of the U.S.D.A., Beltsville, MD, confirmed the identification of the ants. I am grateful to R. SHAW and C BRANDT for statistical advice; to J. GREGG, P. KLOPFER, P. JAISSON and an anonymous reviewer for their comments on the manuscript; and to J. GORDON, R. PALMER and J. GREGG for their help throughout the project.

References

BERNSTEIN R.A., 1975. — Foraging strategies in response to variable food density. *Ecology*, *56*, 213-219.

CARROLL C.R., JANZEN D.H., 1973. — Ecology of foraging by ants. *Ann. Rev. Ecol. Syst.*, *4*, 231-259.

CHEW R.M., 1976. — Foraging behavior of Chihuahuan desert foraging ants. *Am. Midl. Nat.*, *95*, 455-458.

CULVER D.C., 1974. — Species packing in Carribean and north temperate ant communities. *Ecology*, *55*, 947-988.

DAVIDSON D.W., 1977 a. — Species diversity and community organization in desert seed-eating ants. *Ecology*, *58*, 711-724.

DAVIDSON D.W., 1977 b. — Foraging ecology and community organization in desert seed-eating ants. *Ecology*, *58*, 725-737.

DAVIDSON D.W., 1980. — Some consequences of diffuse competition in a desert ant community. *Am. Nat.*, *116*, 92-105.

DE VITA J., 1979. — Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave desert. *Ecology*, *60*, 729-734.

GORDON D.M., 1983. — The relation of recruitment rate and activity rhythms in the harvester ant *Pogonomyrmex barbatus* *J. Kans. Entomol. Soc.*, *56*, 277-285.

HANSEN S.R., 1978. — Resource utilization and coexistence of three species of *Pogonomyrmex* ants in an upper Sonoran grassland community. *Œcologia*, *35*, 109-117.

HARRISON J.S., GENTRY J.B., 1981. — Foraging patterns, colony distribution and foraging range of the Florida harvester ant *Pogonomyrmex badius*. *Ecology*, *62*, 1467-1473.

HÖLLDOBLER B., 1976 a. — Recruitment behavior, home range orientation, and territoriality in harvester ants, *Pogonomyrmex*. *Behav. Ecol. Sociobiol.*, *1*, 3-44.

HÖLLDOBLER B., 1976 b. — The behavioral ecology of mating in harvester ants *(Pogonomyrmex)*. *Behav. Ecol. Sociobiol.*, *1*, 405-423.

RISSING S.W., 1981. — Prey preferences in the desert horned lizard : influence of prey foraging method and aggressive behavior. *Ecology*, *62*, 1031-1040.

SOKAL R.R., ROHLF F.J., 1981. — *Biometry*, 2nd Ed., San Francisco, W.H. Freeman.

SPIEGEL S., 1956. — *Nonparametric statistics for the behavioral sciences*, New York, Mc-Graw-Hill.

TIMM N.H., 1975. — *Multivariate analysis*, Monterey, CA, Brooks/Cole Publishing Co.

WHITFORD W.G., 1978. — Foraging in seed-harvester ants *Pogonomyrmex* spp. *Ecology*, *59*, 185-189.

WHITFORD W.G., ETTERSHANK G., 1975. — Factors affecting foraging activity in Chihuahuan desert harvester ants. *Env. Entomol.*, *4*, 689-696.

WHITFORD W.G., JOHNSON P., RAMIREZ J., 1976. — Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Ins. Soc.*, *23*, 112-132.

WILSON E.O., 1971. — *The insect societies*, Cambridge, MA, Belknap Press.