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Demography and Role of Herbivorous Ants in a Desert Ecosystem as Functions of Vegetation, Soil and Climate Variables

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DEMOGRAPHY AND ROLE OF HERBIVOROUS ANTS IN A DESERT ECOSYSTEM AS FUNCTIONS OF VEGETATION, SOIL AND CLIMATE VARIABLES

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ABSTRACT

The density of harvester ant colonies was found to be a function of number of species of harvester ants in an area and the percent plant cover divided by the number of plant species. It is suggested that this is due to selective foraging behavior of harvester ant species and intra- and interspecific interactions. Mark recapture estimates of forager populations of *Pogonomyrmex rugosus* demonstrated that forager population size in this species is variable, averaging 500-5000 individuals. Imposed mortality studies indicate that predation on foragers could have important consequences on the survival of a colony. Foraging activity and intensity of foraging were shown to vary as a function of combined factors of soil surface temperature (Tss) and saturation deficit (SD) in *P. rugosus* and *Novomessor cockerelli*. *N. cockerelli* is active at Tss between 18°C and 33°C and SD 0 - 30 gms/m^3, while *P. rugosus* extends its activity at Tss of 18°C to 47°C and SD 0 - 52 gms/m^3. A study of foraging range of *P. rugosus* showed that this species forages intensively at distances from 0 - 15 m in an area with a harvester ant colony density of 18/hectare. Techniques for estimating population numbers per colony, foraging activity, and range and effects of predation are discussed and evaluated.

INTRODUCTION

In their study of the bioenergetics of the southern harvester ant, *Pogonomyrmex badius*, Golley and Gentry (1964) found that the energy flow in that species was considerably higher than that of two homeotherms in an old field ecosystem. They estimated that *P. badius* consumed a major portion of the seed production of an old field each year. There are several species of harvester ants in the genera *Pogonomyrmex*, *Novomessor*, *Veromessor* and *Pheidole*, which are common in all North American deserts. Based on our observations and the scant data available in the literature (Tevis, 1958), it is assumed that these insects store and utilize a significant portion of the seed crop in desert areas and due to the large colony size may represent an important component in the energy transfers in desert ecosystems.

The role of harvester ants in a desert ecosystem is not limited to their potential importance in energy flow. Tevis (1958) suggested that *Veromessor pergandii* may influence the abundance of certain plant species by selective foraging for seeds. This hypothesis needs to be examined with regard to several species of harvester ants if simulation of plant species reproduction is to be a goal of a modelling effort. Behavioral relationships and spatial relationships of various species of harvester ants in desert areas need to be elucidated in order to understand their function in desert ecosystems. Our present knowledge of the behavior of harvester ants is largely limited to qualitative observations (Cole, 1934, 1968; Wheeler and Creighton, 1934; Creighton, 1950; and Sudd, 1967).

This study was designed to : 1) evaluate the relationship of ant colony density to vegetation in order to provide a basis for general application of ant data to desert areas; 2) provide insights into the relationships of plants and harvester ant species. Since harvester ants act as selective granivores, scavengers, and occasionally predators, and since they also serve as prey for several invertebrates and vertebrates, their activity, numbers, and harvesting behavior in relation to environmental parameters need elucidation to provide the basis for evaluating their role in a desert ecosystem.

OBJECTIVES

1. To estimate density and study distribution patterns of colonies of species of harvester ants at selected locations in desert areas.
2. To develop techniques for estimation of population numbers and biomass of harvester ant colonies and to calibrate these measurements by actual counts.
3. To develop techniques for and measure activity patterns of harvester ant species as a function of environmental variables.
4. To estimate forager numbers and foraging range.
5. To qualitatively and quantitatively evaluate rate of input of foraged materials to the colony.

METHODS

Relationships of harvester ants to species composition and structure of the plant community were determined in selected areas of three deserts (Chihuahuan, Sonoran, and Mohave). By means of the wandering quarter method (Cantana, 1963), the density of ant colonies was measured in relation to height and canopy of nearest shrubs, and the line intercept method was employed to determine species composition of the sites (DSCODE A3UEE01). The samples were taken at random.

A mark-recapture method was used to estimate forager population of colonies of harvester ants selected at random in the Chihuahuan Desert. In order to relate this to number of ants in a colony, colony population was estimated by restricting a colony's food supply to fluorescent-dyed seeds, then measuring fluoresence per ant after an interval of 5 days and applying the dilution factor. The colony was forbidden a food source for 5 days before providing the dyed seed. These measurements were made on colonies of *Novomessor cockerelli*, *Pogonomyrmex rugosus*, *P. californicus*, *P. maricopa*, and *P. desertorum* (DSCODE A3UEE02).

The study of environmental factors regulating harvester ant activity was undertaken at the Jornada site and on areas near New Mexico State University. Intensity of foraging activity was measured as a function of soil surface temperature, humidity near the soil surface, light intensity, and food availability (DSCODE A3UEE03). The last parameter was manipulated by providing seeds near the nest. Foraging activity was determined in part by removal of seeds and partly by the number of ants returning to the nest per unit time. Selected colonies were examined in this experiment from the species listed in preceding paragraph. In a related study (DSCODE A3UEE04) on the same sites, foraging range and potential overlap of foraging range of adjacent nests were assessed. These objectives were obtained by placing seeds dyed with different colors at fixed distances from the nest, measuring the number of each color brought to the nests, and noting distances to the nearest nest in each quarter recorded.

FINDINGS & DISCUSSION

Ant Colony Density -- Vegetation Relationships

Before foraging relationships of various harvester ant species can be understood, it is necessary to understand the spatial relationships of ant colonies and the relationships of ant colony density to the plant community. Considerable effort was expended in order to obtain data to provide insight into these relationships.

Figure 1 presents the results of a regression analysis of a productivity-species diversity index and colony density-diversity index. This analysis gave an r^2 value of 0.90. Analysis of these data by plotting nest density against the certain parameters -- percent cover, shrub density, shrub cover, and grass and forb cover -- showed that in each case colony density from two or three of the areas studied varied as a function of the parameter selected for analysis, as can be seen in Table 1.

Harvester ant colony density appeared to be a function of number of harvester ant species in an area and cover and diversity of vegetation in a given area. To test this, these parameters were included in the analysis by dividing colony density by the number of species sampled in that area and by dividing the percent cover by the number of species encountered in our cover estimates. While this treatment of the data may be considered somewhat extreme, it is expected to be relevant to the ecology of harvester ants in view of the following considerations:

(1) Plant communities with high-percent plant cover and low species diversity, such as the shadscale community in Curlew Valley, may present harvester ants with most of the production in an unpalatable form such as *Halogeton glomeratus*. In a more complex community such as the sage community in Curlew Valley, there is a greater probability that much of the production is in a palatable form, either as seeds to the ants or in supporting insect populations which supply these species with the protein necessary for reproduction.

Table 1. Harvester ant nest density, harvester ant species diversity, and plant cover, density, and species diversity in the areas surveyed.

Area	No. of nests/hectare	Ant Species	Ant Species % total	% Cover all plants	# Plant species	Shrub density #/hectare	% Shrub cover	# Shrub species	Grass & forb cover	# Grass & forb Species
Big Bend, Tex.	36.6	NOVCOC POGRUB	14.6 85.4	42.5	37	2537	19.34	26	23.14	11
Las Vegas, Nev.	3.58	POGRUG	100	14.5	19	3084	11.96	13	2.54	6
Curlew Valley (sage)	72.93	POGOWY	100	52.82	9	541	7.5	6	45.3	3
Curlew, Utah Shadscale	17.9	POGOWY	100	48.79	14	2551	15.6	4	33.15	10
Portal, Ariz.	63.5	NOVCOL POGBAR POGCAL PHEISP	29.3 27.8 10.9 6.2	32.1	15	1128	22.2	7	9.9	8
Portal, Ariz. Chained area	30.8	POGBAR NOVCOC	66.7 33.3	40.0	14	--	3.71	2	36.26	12
Four Corners, N.M.	25.4	POGRUB	100	11.8	11	453	7.5	5	4.3	6
Jornada Plava fringe	24.2	NOVCOC POGRUG POGCAL POGDES	23.3 53.3 13.3 10.0	29.7	26	1466	21.4	6	8.3	20
Four Corners N.M.	12.5	POGRUG	100	6.2	7	--	2.7	3	3.5	4

NOVCOC - *Novomessor cockerelli*
POGRUG - *Pogonomyrmex rugosus*
POGOWY - *Pogonomyrmex owyheei*
POGBAR - *Pogonomyrmex barbatus*
POGCAL - *Pogonomyrmex californicus*
POGDES - *Pogonomyrmex desertorum*

(2) In an area with similar production (cover) and plant species diversity, we should expect colony density to vary as a function of harvester ant species diversity. Nest spacing (which directly affects density) is fairly uniform in areas where but one species of harvester ant is found, e.g. Curlew Valley (Utah), Las Vegas (Nevada), Four Corners (New Mexico). However, where two or more species are found, colony spacing is not uniform. For example, *P. rugosus* nests are often found less than 10 meters from a *N. cockerelli* nest. As shown later, the foraging activity cycles of these species are partially out of phase, thus reducing competition.

It is suggested, therefore, that plant diversity and production and the degree of intra- and interspecific competition between harvester ant species are the factors which regulate colony density.

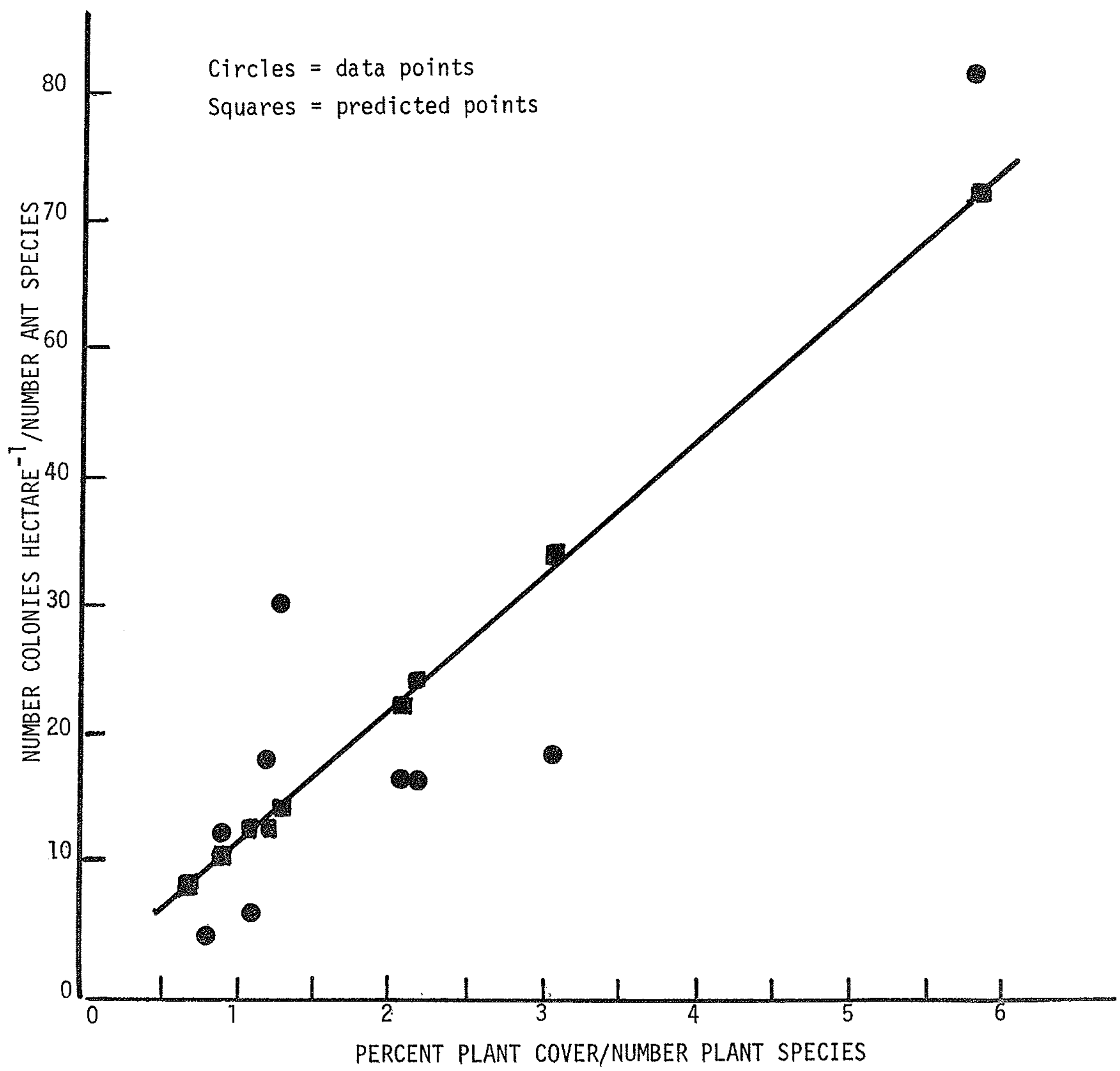


Figure 1. The relationship of harvester ant colony density and number of harvester ant species encountered, and percent plant cover per number of plant species intercepted.

Population Numbers -- Harvester Ant Colonies.

Considerable time was spent on this portion of the study in developing techniques. Laboratory colonies were established on which to test various labeling techniques in an attempt to find a method which would be feasible to use and calibrate in the field.

Attempts to use radioactive tracer dilution as a method of assessing colony numbers proved unsuccessful. After obtaining a fluorimeter, tests were run on the use of rhodamine B-treated grain passed on to the other colony members by foragers to assess colony numbers. The results of these tests with three laboratory colonies of *P. maricopa* are shown in Table 2.

Table 2. Estimated population numbers by use of rhodamine B fluorescent marker and actual numbers in the colony.

Colony	Estimated #	Actual #	% Error
1	1407	1608	12.5%
2	1361	1906	28.6%
3	1193	1363	12.5%

Two possible sources of error were considered in these preliminary studies: (1) in transferring the colonies, some of the labeled food was lost, and (2) in trials 2 and 3 the food was heavily dyed and may have had reduced palatability. This technique will be tested further and field calibration will be run.

Estimates of forager population numbers by paint spot mark-recapture techniques also presented problems in technique development such as selection of non-toxic paints, slowing the animals for marking without affecting their recovery and survival. The latter problem was solved by cooling the ants in a plastic container held over ice. The technique is time-consuming but appears to be effective in obtaining estimates of forager numbers.

Table 3 summarizes the data on forager population numbers of several harvester ant colonies. The great differences seen in forager population estimates from different dates is explained in part by the probable higher mortality of multiple-marked animals due to handling and excess paint. Therefore, the first estimates for a colony are considered to be more reliable. In the future, emphasis will be given to single period mark-recapture and Lincoln-Petersen Index forager population estimates. These data do demonstrate that there is considerable variation in forager population numbers within colonies of the same species. During the next season of activity an attempt will be made to correlate forager population size with some parameters such as nest size, etc.

In any study of the dynamics of a social insect such as harvester ants, the recruitment of new foragers to replace foragers lost by predation or other mortality is an important consideration. Immediate replacement from the colony pool to keep foragers at a fixed percentage of the colony would insure a rate of supply of food material commensurate with the colony's needs. Failure to replace the foragers could result in debilitation and eventual death of the colony. Two experiments were attempted to assess colony response to imposed mortality of half the estimated forager population. The results of these efforts are summarized in Table 4. Imposed mortality caused a drop of over 1/3 below the expected forager population without recruitment in the larger colony and resulted in apparent demise of all foragers in the smaller colony. This may be due to normal reduction in forager numbers at this season or to lack of reproduction due to dry conditions and subsequent failure to recruit foragers. This approach appears to provide a basis for insight into colony population dynamics and will be expanded in the coming year.

Table 3. Estimates of forager population numbers for selected ant colonies in the playa fringe area. Codes refer to nest location coordinates on the master map of the study area.

Species	Location Coordinates	Sample Date	Population Estimate
Pogonomyrmex rugosus	75N 37.5E	July 10	555
		July 11	379
Pogonomyrmex rugosus	65N 32.5E	July 11	611
	100N 600E	July 26	1000
		July 28	731
		July 30	1106
Pogonomyrmex rugosus	200N 375E	July 26	5000
		July 28	2292
		July 30	1516
Novomessor cockerelli		August 22	1429
		August 23	2442

Table 4. Estimates of forager population before and after imposed mortality.

Species	Sample Date	Treatment	Population Estimate
Pogonomyrmex rugosus	August 2	none	909
	August 3	none	1313
	August 4	none	846
	September 6	removed 455 foragers	
	September 11	none	261
Pogonomyrmex rugosus	August 2	none	303
	September 6	removed 151 foragers	
	September 11		0
	September 12		0

Environmental Factors Affecting Harvester Ant Foraging Activity:

At the beginning of these studies, only soil surface temperature was measured concurrently with foraging activity. After several observations of increased activity of all species of harvester ants following light rains, measurement of moisture conditions at the soil surface was attempted in addition to soil surface temperatures. A Lithium Chloride Hygrometer was borrowed for these measurements, which proved to be most valuable in evaluating factors affecting foraging activity.

Data on the effects of soil surface temperature and saturation deficit on foraging activity of the dominant species of harvester ants in the Chihuahuan desert are summarized in Figures 2 and 3. *Pogonomyrmex rugosus* is active at high saturation deficits (s.d.) and high temperatures, while activity for *Novomessor cockerelli* is restricted to periods of more moderate temperatures and s.d.'s. Neither species was found actively foraging at temperatures below 15°C. S.d.'s below 4.8 gm/m^3 were not measured so it is not certain whether activity ceases below this point. *N. cockerelli* exhibited nocturnal foraging in summer, thus avoiding high temperatures. More data are necessary to accurately evaluate diel periodicity separate from temperature and moisture considerations in these species.

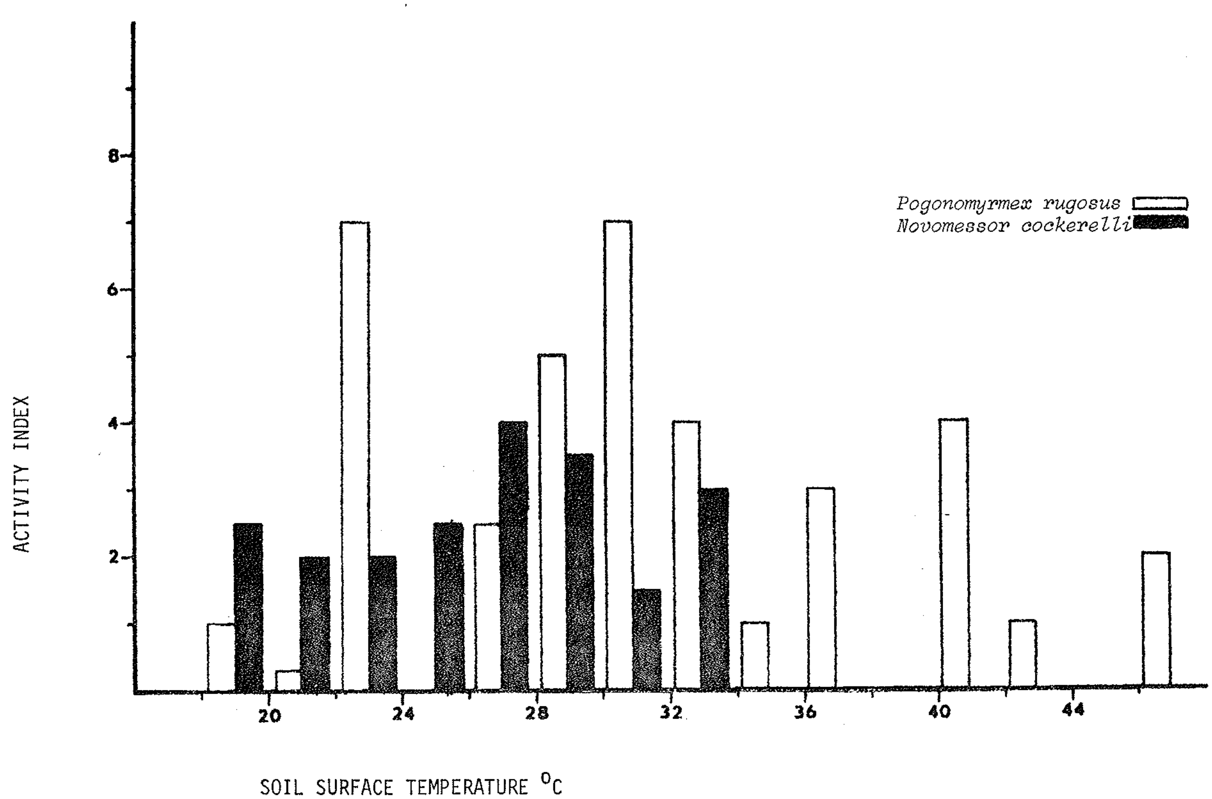


Figure 2. The influence of soil surface temperature on foraging activity of two species of harvester ants. Activity index equals the number of foragers returning to the nest in four minutes.

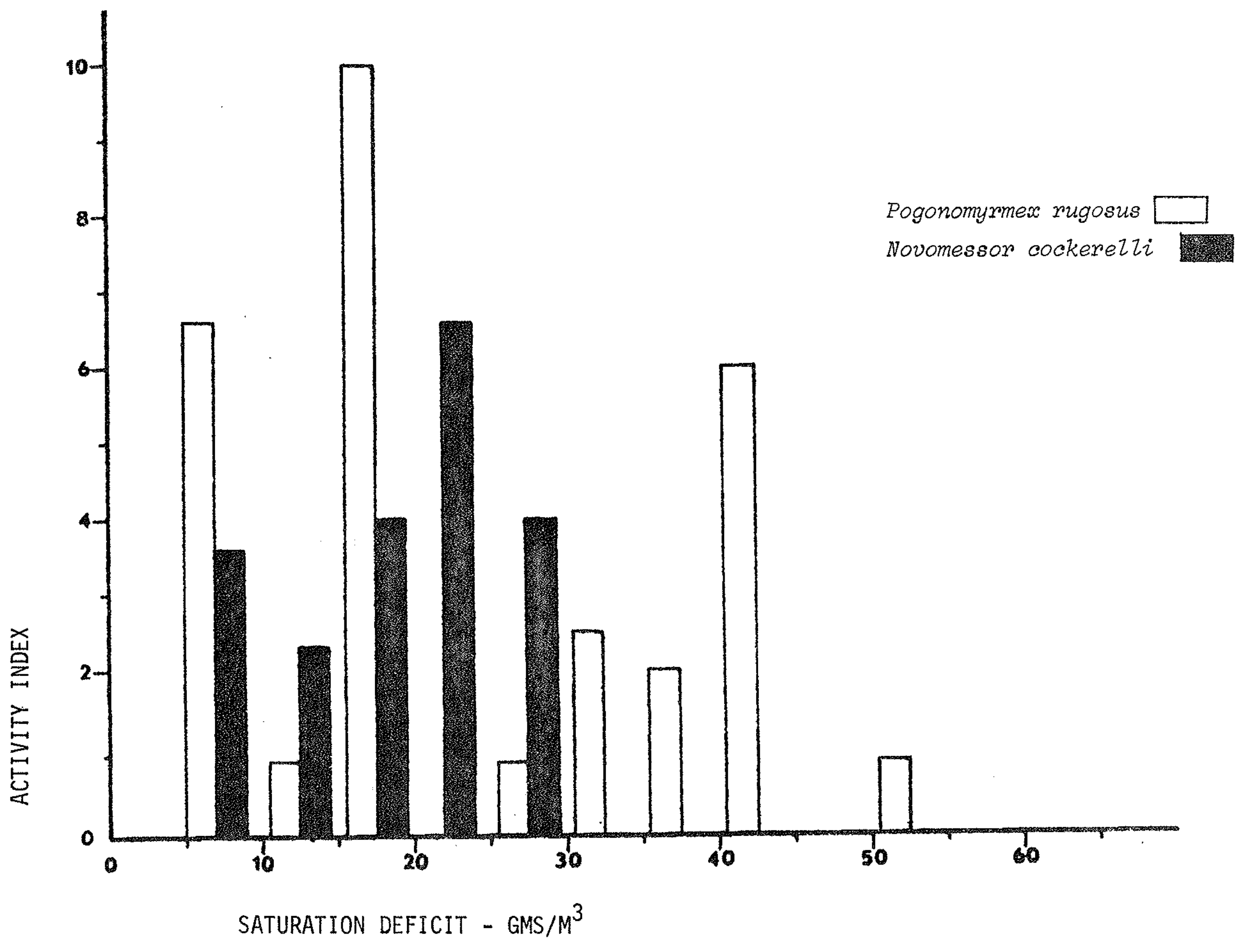


Figure 3. The influence of saturation deficit on foraging activity of two species of harvester ants. Activity index equals the number of foragers returning to the nest in four minutes.

The factors affecting foraging activity are combined in Figures 4 and 5 to provide an activity tolerance surface on which to base prediction of foraging behavior. Examination of these Figures demonstrates that while there is almost complete overlap of peak activity at s.d.'s between 0 and 30 and soil surface temperatures between 20°C and 35°C in both species, *P. rugosus* continues to forage, but at reduced levels, at s.d.'s greater than 30 gm/m^3 and soil surface temperatures greater than 35°C. These differences in foraging activity patterns are obvious factors reducing competition between these species.

Tevis (1958) reports that *Veromessor pergandii* was barely mobile at 13°C and very active at 33°C. His study provided no data on moisture levels and foraging, nor intensity of foraging. He did report that night foraging was rare and that *V. pergandii* foraged up to 40m from the nest. Comparisons with data in Tevis (1958) indicate that the activity and foraging behavior of *V. pergandii* is similar to that of *P. rugosus*. In a study on activity of *Pheidole* in a grassland-shrub community in Tanganyika, Kemp (1951) reported that *Pheidole* foraged between 0600 and 2100 hours with decreased activity at midday. However, he presented no environmental data with which to compare findings on *P. rugosus* and *N. cockerelli*. In his review on the behavior of ants, Sudd (1967) suggests that both moisture and temperature are factors affecting behavior of arid zone ants, but this suggestion was based on scant data. Thus, it is evident that soil surface temperature-s.d. models should be provided for most species of harvester ants to provide the basis for predicting foraging activity.

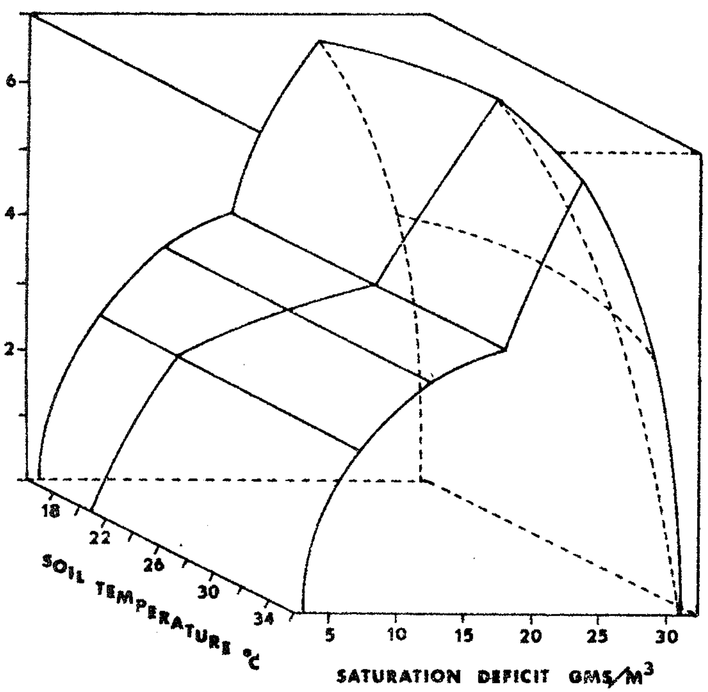


Figure 4. Soil temperature-saturation deficit levels at which *Novomessor cockerelli* forage.

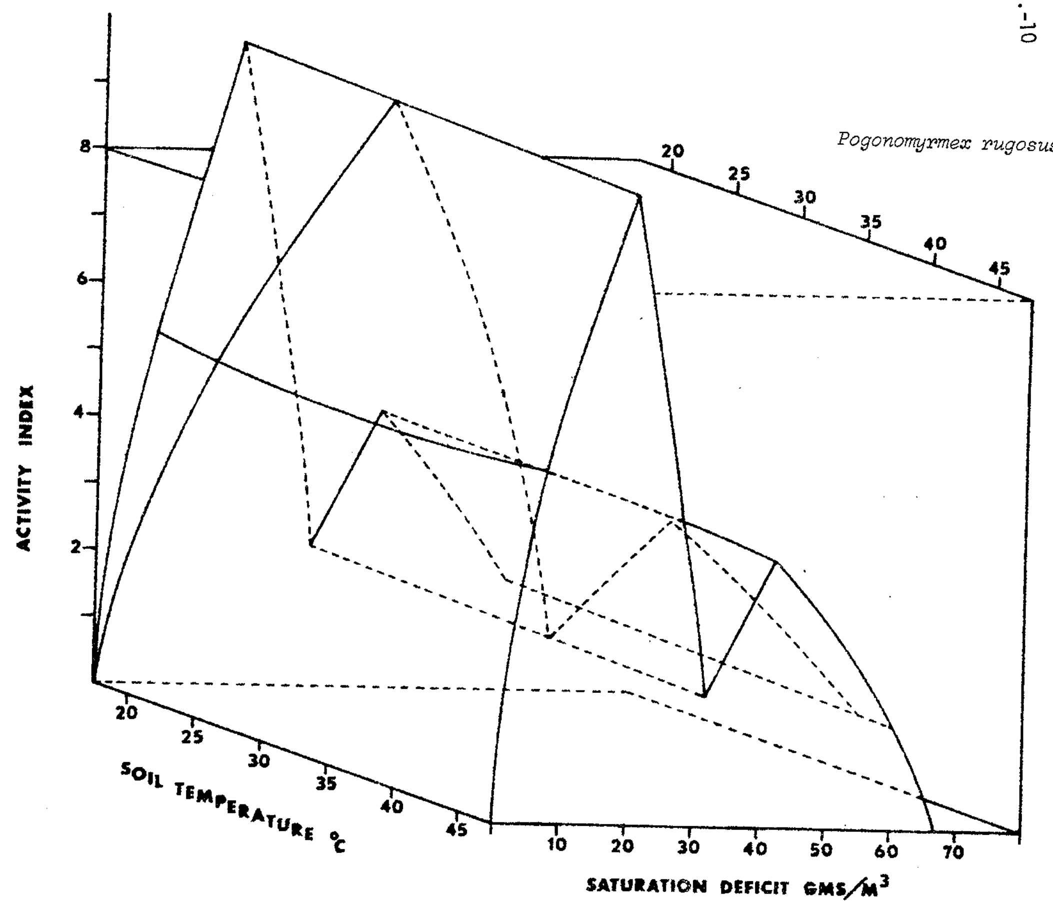
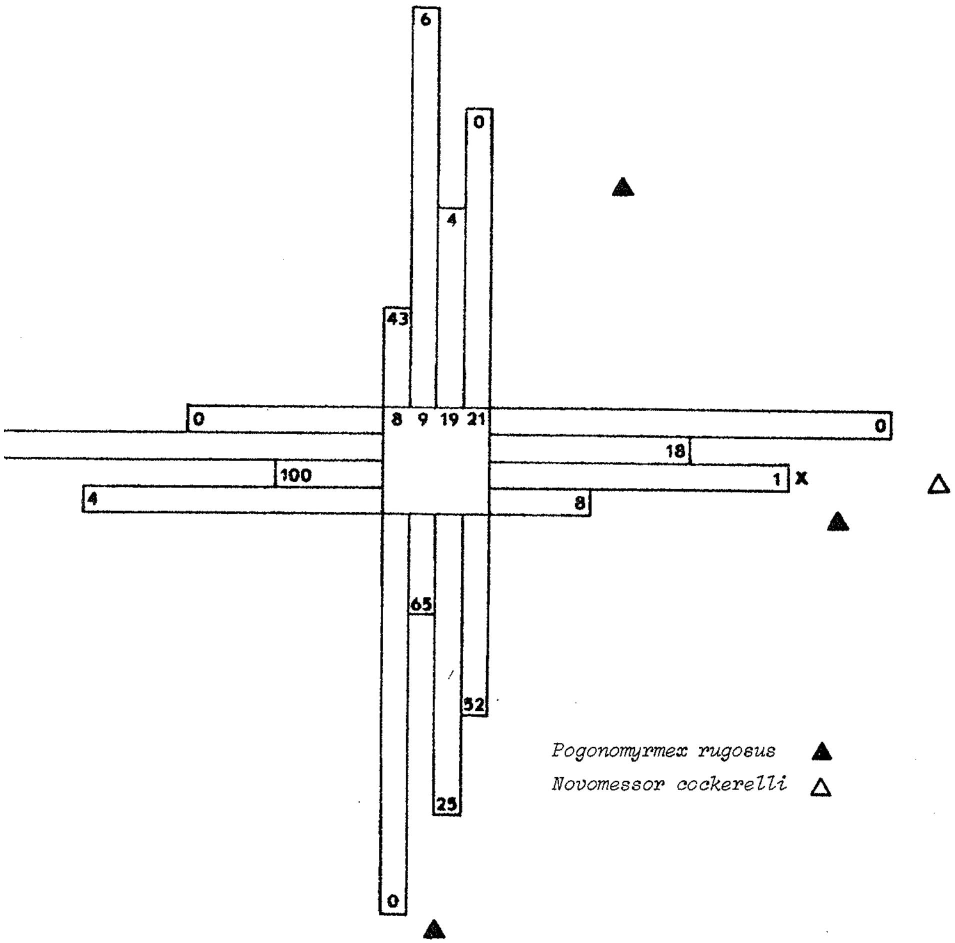


Figure 5. Soil temperature-saturation deficit levels at which *Pogonomyrmex rugosus* forage.

Foraging Range -- *Pogonomyrmex rugosus:*

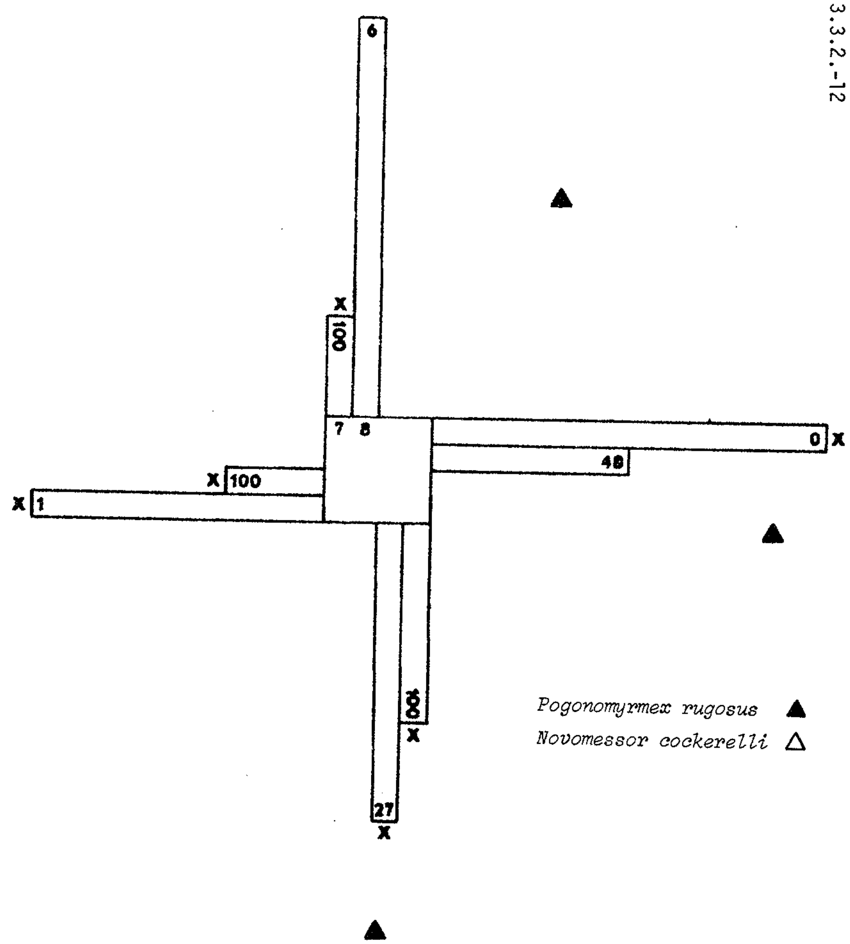
Data on foraging range studies on four colonies of *Pogonomyrmex rugosus* are summarized in Figures 6-9. Several factors affecting foraging range of harvester ants are evident from an examination of these figures. First, the effectiveness of foraging activity is a function of ambient conditions. Thus, when humidities were high and temperatures favorable for foraging, e.g. July 21 and 23, between 0700 and 100 hours, high percentages of seeds were returned to the nest from the nearest areas. However, when the temperature dropped below 20°C, foragers harvested very few seeds even from a distance of 7.5 meters. These data also indicate foraging range overlap between colonies of the same species and different species, i.e. *Novomessor cockerelli*. In order to quantify the relationship, distance to a food source and distance to another harvester ant colony, it will be necessary to repeat these studies with observers at all nests within the maximum foraging distance. It is also apparent that foraging range may vary as a function of colony density and primary production. The results of our studies to date indicate that in an area with a colony density of 18/hectare there is foraging overlap, but that the average intense foraging range is between 7.5 and 15 meters. Therefore, these studies will be expanded and repeated in an area with low ant colony density and the placement of dyed seeds varied to more accurately evaluate degree of overlap of foraging range between colonies.

Table 5 summarizes the data on materials returned to *P. rugosus* nests during the foraging range studies. The percent of the total of seeds returned to the nest is approximately the same as the percent composition of the plant species in the adjacent community. Plants present in the area not represented by materials collected by foragers include several forbs, mesquite, and four-winged saltbush. The ants brought *Cucurbita* seeds to the nests, but removed them soon after they were brought in. Observations during these studies and other general observations support the premise that harvester ants will scavenge other insects or even act as predators on termites whenever possible.



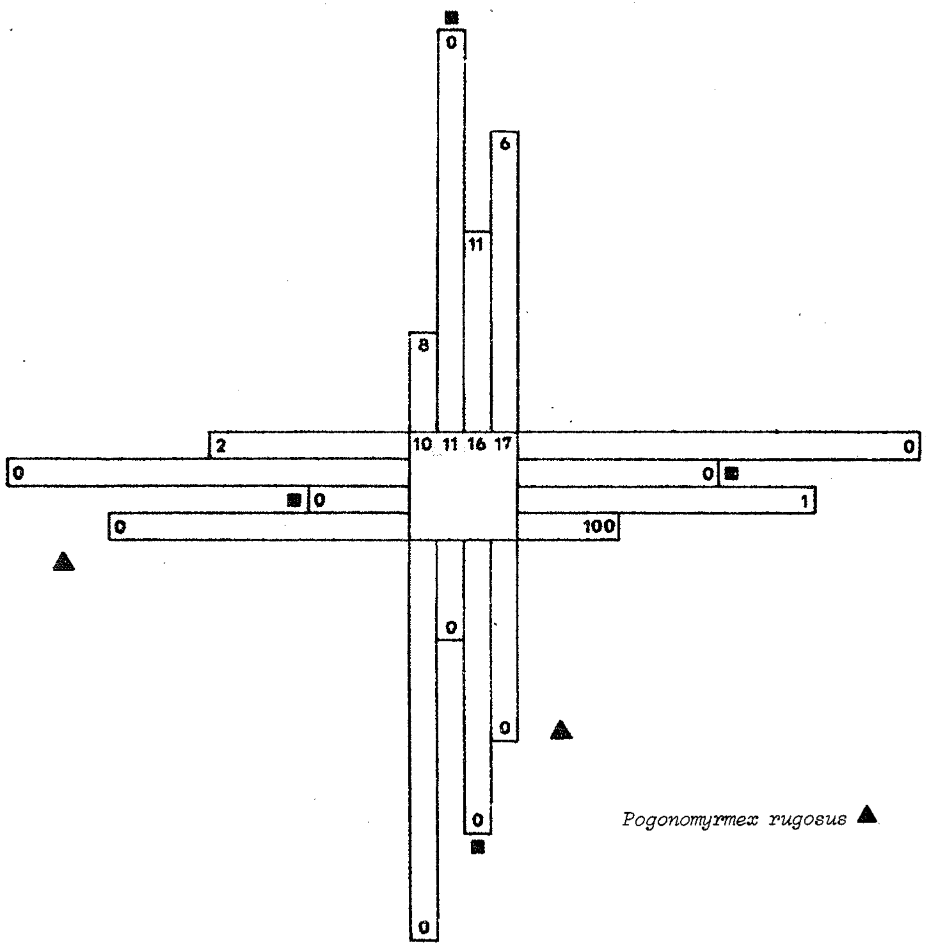
July 21

Figure 6. Foraging range of a colony of *Pogonomyrmex rugosus* as determined by return of dyed seeds in 1 hr. Length of bar indicates distance of dyed grain from the nest, e.g., 7.5m, 15m, 22.5m, and 30m. The number in the open bar equals the percent dyed grain returned of the approximately 100 grains placed in an area. Within the central square, numbers at the base of the bars indicate the time at the beginning of observations (MDT). Times on all other segments are the same, reading clockwise. Triangular symbols indicate approximate position of nearest colonies. An "X" indicates that all seeds from that position were harvested within the hour.



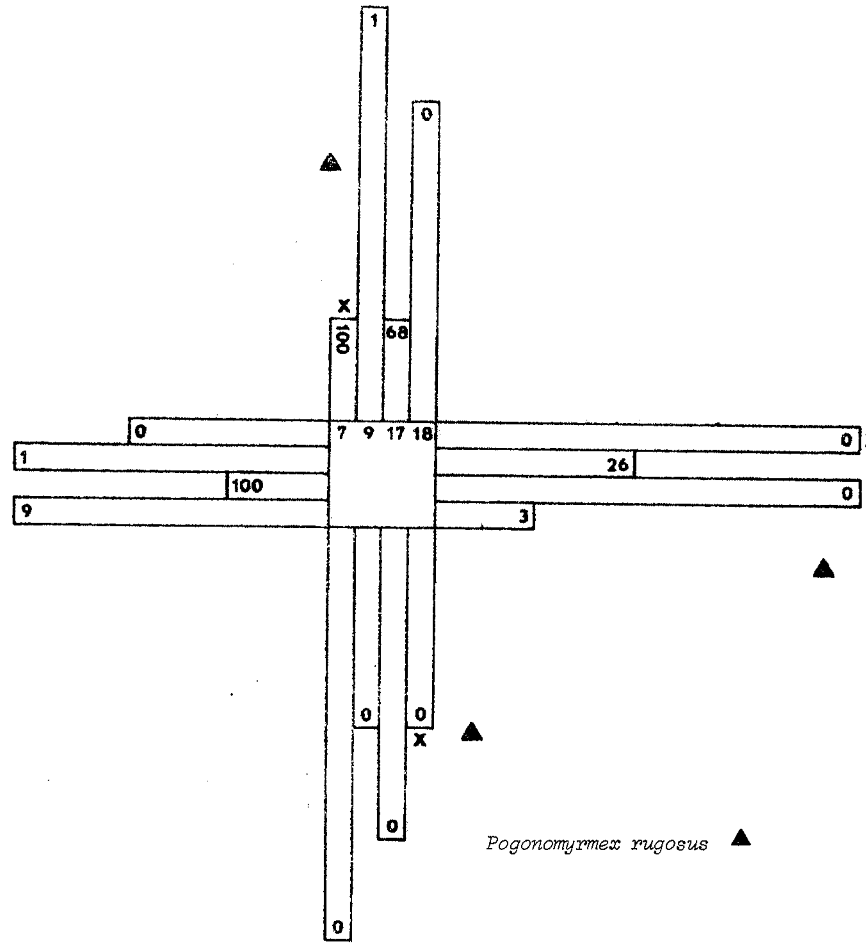
July 23

Figure 7. Foraging range of a colony of *Pogonomyrmex rugosus* as determined by return of dyed seeds in one hour. Method of presentation same as Figure 6.



August 4 and 16

Figure 8. Foraging range of a colony of *Pogonomyrmex rugosus* as determined by return of dyed seeds in one hour. Method of presentation same as Figure 6.



August 6 and 9

Figure 9. Foraging range of a colony of *Pogonomyrmex rugosus* as determined by return of dyed seeds in one hour. Method of presentation same as Figure 6.

Table 5. Materials other than dyed grain brought to nests of *Pogonomyrmex rugosus* during forager range studies.

	Number													
Date	7/21		7/23		7/27		8/4		8/6	8/9	8/16			
Period	(3)	(4)	(1)	(2)	(1)	(2)	(1)	(2)			(1)	(2)		
Species of seed or materials													Sum	%
Ephedra trifurca	2			1	1	1							5	4.5
Yucca elata				2									2	1.8
Curcurbita foetidissum			1	1						6	1		9	--
Cow feces				1									1	0.9
Insects		9			1		1		1				12	10.8
Termites					5		2						7	6.3
Larrea divaricata					2								2	1.8
Rabbit pellets					3				1				4	3.6
Hilaria mutica	5	0	13	17	3	8	6	2	6	0	17		87	70.3

EXPECTATIONS

1. During 1972 emphasis will be focused on adding data on factors affecting foraging activity such as food availability and time of day in addition to saturation deficit and soil surface temperature. This should provide fairly precise limits to foraging and rates of foraging as a function of the pertinent factors for the three important harvester ants in the area: *Pogonomyrmex rugosus*, *Novomessor cockerelli* and *Pogonomyrmex californicus*. Data will be obtained on other species if time permits.

2. The fluorimeter technique will be field-tested for assessing colony size and forager populations manipulated by imposed mortality. It is hoped to establish a ratio between forager population size and colony size which can provide a basis for understanding dynamics of individual colonies. This work will require some colony excavation which is very expensive in terms of manpower.

3. Forager ranges will be studied in an attempt to quantify and predict range and colony overlap in foraging.

4. Techniques will be developed for assessing seed selection and seed removal as a function of seed production, both qualitative and quantitative.

5. Laboratory studies of metabolisms, ingestion and egestion rates will be performed as time permits.

LITERATURE CITED

Cantana, A.J., Jr. 1963. The wandering quarter method of estimating population density. Ecology 44:349-360.

Cole, A.C., Jr. 1968. Pogonomyrmex Harvester Ants: A Study of the Genus in North America. University Tennessee Press. Knoxville. 222 pp.

Cole, A.C. 1934. An ecological study of the ants of the southern desert shrub region of the United States. Ann. Ent. Soc. Amer. 27:388-405.

Creighton, W.S. 1950. The ants of North America. Bull. Mus. of Comp. Zoo. 104:1-585.

Golley, F.B. and J.B. Gentry. 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. Ecology. 45:217-225.

Kemp, P.B. 1951. Field observations on the activity of Pheiodole. Bull. Ent. Res. 42:201-206.

Sudd, John H. 1967. An Introduction to the Behavior of Ants. Edward Arnold, Ltd., London. 200 pp.

Tevis, L., Jr. 1958. Interrelations between the harvester ant *Veromessor pergandii* (Mayr) and some desert ephemerals. Ecology. 39:655-704.

Wheeler, W.M. and W.S. Creighton. 1934. A study of the ant genera *Novomessor* and *Veromessor* Proc. Amer. Acad. Arts & Sci. Boston. 69:341-387.