

# Foraging Ecology of Seed-harvesting Ants, *Pheidole* spp. in a Chihuahuan Desert Ecosystem

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**ABSTRACT:** Seasonal activity, factors affecting foraging activity and forage selection were studied in three species of *Pheidole* (Hymenoptera: Formicidae) on a watershed in the southern New Mexico Chihuahuan Desert. *Pheidole* spp. exhibited a seasonal pattern in numbers of active colonies with most colonies active in July coincident with onset of summer rains and seed drop by annual plants. *Pheidole militica* occurred only on the deeper soils of the lower watershed while *Ph. rugulosa* and *Ph. xerophila* occurred on the entire watershed. The three *Pheidole* spp. were active only at soil temperatures between 15-35°C and were most active at sunrise. Analysis of factors affecting foraging intensity using a stepwise discriminant function and regression showed evaporation and soil surface temperature to be the strongest influences and seed availability to rank second. However, the factors included in the analysis accounted for less than 50% of the variance in all three species. *Pheidole militica* collected mostly forb seeds while *Ph. xerophila* utilized primarily grass seeds, especially the seeds of fluff grass *Erioneuron pulchellum*.

## INTRODUCTION

Seed-harvesting ants (*Pogonomyrmex* sp., *Veromessor pergandii* (Mayr) and *Pheidole* sp.) are important components of desert ecosystems (Whitford, 1978; Davidson, 1977). The ecology of *Pogonomyrmex* sp. has been studied extensively by Whitford (1976, 1978), Whitford *et al.* (1976), Whitford and Ettershank (1975) and Rogers (1974). Tevis (1958), Went *et al.* (1972), Clark and Comanor (1973), Wheeler and Rissing (1975a, b,) and Rissing and Wheeler (1976) reported on aspects of the ecology of *Veromessor pergandii*. However, studies on the foraging ecology of desert-inhabiting species of *Pheidole* are limited (Davidson, 1977). Studies of *Pheidole* are necessary to assess the relative impact of seed-harvesting ants in desert ecosystems. Brown and Davidson (1977) showed that the density of *Pheidole* sp. increased in areas where seed-eating rodents were excluded, indicating that these seed harvesters responded quickly to the removal of competitors whereas the large-body-size, seed-harvesting ants of the genus *Pogonomyrmex* appeared not to be affected. The work of Brown and Davidson suggests potentially important differences between *Pheidole* and *Pogonomyrmex* and point to a need for information concerning the foraging ecology of desert species of *Pheidole*. Our studies were designed to examine the foraging ecology of *Pheidole militica* (Wheeler), *Pheidole rugulosa* (Gregg) and *Pheidole xerophila* (Wheeler), the most numerous species of *Pheidole* in several plant communities on a Chihuahuan desert watershed.

## METHODS

Studies were conducted on the Jornada Validation Site watershed 40km NNE of Las Cruces, Dona Ana Co., New Mexico. The watershed is an alluvial fan to the N and E of Mt. Summerford, Dona Ana Mountains, which drains into a small ephemeral lake. The upper portion of the watershed at the base of the mountain (elevation ca. 2000 m) is a black grama (*Bouteloua eriopoda*) (Torr.) grassland which shifts abruptly to a creosote bush (*Larrea tridentata*) (DC)-dominated desert pavement community on shallow soils. On the highly dissected slopes of the watershed, the creosote bush community supports a variety of annual plants which occur at low densities during summer rainy periods (ca. 10,000·ha<sup>-1</sup>) (Whitford, 1973).

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The deeper sandy loam soils around the ephemeral lake are dominated by mesquite (*Prosopis glandulosa*) (Torr.), long leaf mormon tea (*Ephedra trifurca*) (Torr.) and creosote bush. This area supports high densities of annual plants (ca. 100,000 ha<sup>-1</sup>) during rainy periods in the growing season.

One 400 m<sup>2</sup> plot was selected in each of the different plant communities. Ant colonies were identified to species when major workers were on the surface, assigned a number, and tagged by a wire marker adjacent to the nest disc. These colonies were examined at least every 2 weeks to determine seasonal variation in activity.

Foraging intensity was studied by counting the number of foragers returning to the colony in 2 min. Five colonies of each species were chosen at random and foraging activity estimates were made at 2-hr intervals from initiation of foraging in the late afternoon ca. 1800 hr to 2400 hr and from ca. 0500 hr until foraging ceased. Soil surface temperature was recorded at the beginning of each counting period by covering the bulb of a thermometer with a thin layer of soil. Relative humidity was measured with a sling psychrometer. The number of ants with visible forage in their mandibles was also recorded.

The composition of forage carried by the three species of *Pheidole* workers was estimated by removing forage items from returning workers. This was difficult because workers tended to drop their forage when disturbed before the worker and its food item could be picked up. We collected forage from 50-100 individual workers of 5-6 colonies of *Ph. xerophila* on both the upper and lower watershed and *Ph. militicida* only on the lower watershed. Problems of consistently collecting forage from *Ph. rugulosa* prevented us from including a comparison with this species. We compared the percent composition of forage collected from returning workers with the percent composition of parts in trash piles near the nests and found them to be very similar.

The critical thermal maxima (CTMax) were estimated by heating 20-25 individuals of each species of worker at a constant rate (1 C per min) until the individual lost coordinated movement. The arithmetic mean of the temperatures at which ants lost coordinated movement was used as the CTMax. We analyzed the 1976 data using a stepwise discriminant function and regression using the principal components programs of the BMDP package on an IBM 36-65 computer.

## RESULTS

*Pheidole* spp. exhibited a definite seasonal pattern in numbers of active colonies. This seasonal pattern appeared to be related to rainfall and the growth and seed set of annuals. Peak activity in all *Pheidole* spp. occurred in July coincident with the onset of summer rains and with seed set by annual plants which had grown in response to 43.4 mm of rainfall on 4 and 6 June (Table 1). Prior to June there was very little foraging activity by the species of *Pheidole* and major workers were not seen in those few colonies exhibiting activity until July. Between mid-March and June we found 1-2 colonies or fewer per plot that were active. June rains appeared to serve as a stimulus to activity and appearance of major workers.

Less than one fourth of the colonies remained active after the onset of freezing nighttime temperatures in October. There was variation in the seasonal pattern within a species. A few colonies which were active in July but inactive in August were active in October and November. However, most of the colonies active in October and November were active on most sampling days from late June through November, i.e., 70% of the *Pheidole xerophila* and 60% of the *Ph. rugulosa*. Colonies of *Pheidole* spp. active October-December switched from largely nocturnal to midday activity and limited their activity to days in which soil surface temperatures exceeded 20°C.

The *Pheidole* spp. of the Jornada were most active at dawn (between 0430-0600 hr MDT) and the 1st 3 hr after sunset (between 1900-2100 hr MDT) (Fig. 1). *Pheidole militica* continued activity until late morning during periods when soil surface temperatures remained below 34 C. *Ph. rugulosa* and *Ph. militica* maintained relatively constant foraging intensity throughout the activity period. *Pheidole xerophila* exhibited peak foraging intensity in the early evening (Fig. 1). Although peak foraging intensity occurred early in the evening, the number of colonies which were active peaked in the early morning hours (Fig. 1).

The critical thermal maximum  $\pm 1$  SD of the minor workers of the three *Pheidole* spp. was  $46 \pm 1.8$  C. Since there was no difference (in CTMax) among species, all were lumped in the analysis.

*Pheidole* spp. were active only at soil surface temperatures between 15 - 35 C but at a variety of relative humidities (Fig. 2-4). There was considerable variation in foraging intensity at all temperature and humidity combinations within these bounds. We attempted to ascertain those factors which regulate foraging intensity in *Pheidole*. Variables included in the analysis were: time of day, soil surface temperature, relative humidity, maximum and minimum temperatures, the average of maximum and minimum temperatures over the previous 3 days, rainfall in the previous 7 and 14 days, cumulative annual rainfall to date, evaporation in the previous 24 hr, kilometers of wind in the previous 24 hr and Julian day of the year. A synthetic variable expressing the Julian day as a cosine function to simulate vegetative productivity was also used. We attempted to discriminate between species by examining the relationship between each species and the first two canonical variables. The first

TABLE 1.—Percent of the estimated maximum number of active colonies of *Pheidole* spp. in the various habitat types on the Jornada during the period of activity in 1976. The number in parentheses below the species is the maximum density in numbers of colonies·ha<sup>-1</sup> in that habitat

Species	June		July		August		Sep.	Oct.	Nov.
	1-15	16-30	1-15	16-30	1-15	16-30			
	Creosote bush (shallow soil)								
<i>Ph. rugulosa</i> (225)	57	36	93	100	43	64	43	7	7
<i>Ph. xerophila</i> (300)	56	13	100	100	56	63	19	6	6
	Creosote bush (deep soil)								
<i>Ph. rugulosa</i> (350)	66	35	100	89	56	44	33	22	11
<i>Ph. xerophila</i> (400)	58	33	100	100	33	58	25	33	22
	Mesquite mormon tea (deep soil)								
<i>Ph. militica</i> (100)	50	0	100	50	50	50	25	0	25
<i>Ph. rugulosa</i> (150)	33	0	100	100	67	67	40	0	9
<i>Ph. xerophila</i> (325)	57	31	100	78	38	54	23	23	15
	Grama grassland								
<i>Ph. rugulosa</i> (500)	60	10	100	100	78	63	45	16	0
<i>Ph. xerophila</i> (1300)	78	13	100	100	90	76	41	43	31

Rainfall in mm for months indicated; numbers in ( ) are the number of rain events. Apr. 15.24 (2), May 24.13 (3), June 43.43 (2), July 53.9 (5), Aug. 14.4 (3), Sept. 31.8 (3), Oct. 9.91 (3), Nov. 15.24 (1)

canonical variable provided the greatest separation of the species (correlation coefficient = 0.571) but there was considerable overlap between species. The coefficients of the variables show that for the first canonical variable the strongest influences are evaporation and soil surface temperatures. The second canonical variable (correlation coefficient = 0.295) reflects the seasonality of seed availability.

The regression of foraging intensity and foraging success (number of ants with forage per unit time) on the principal components of the physical environment

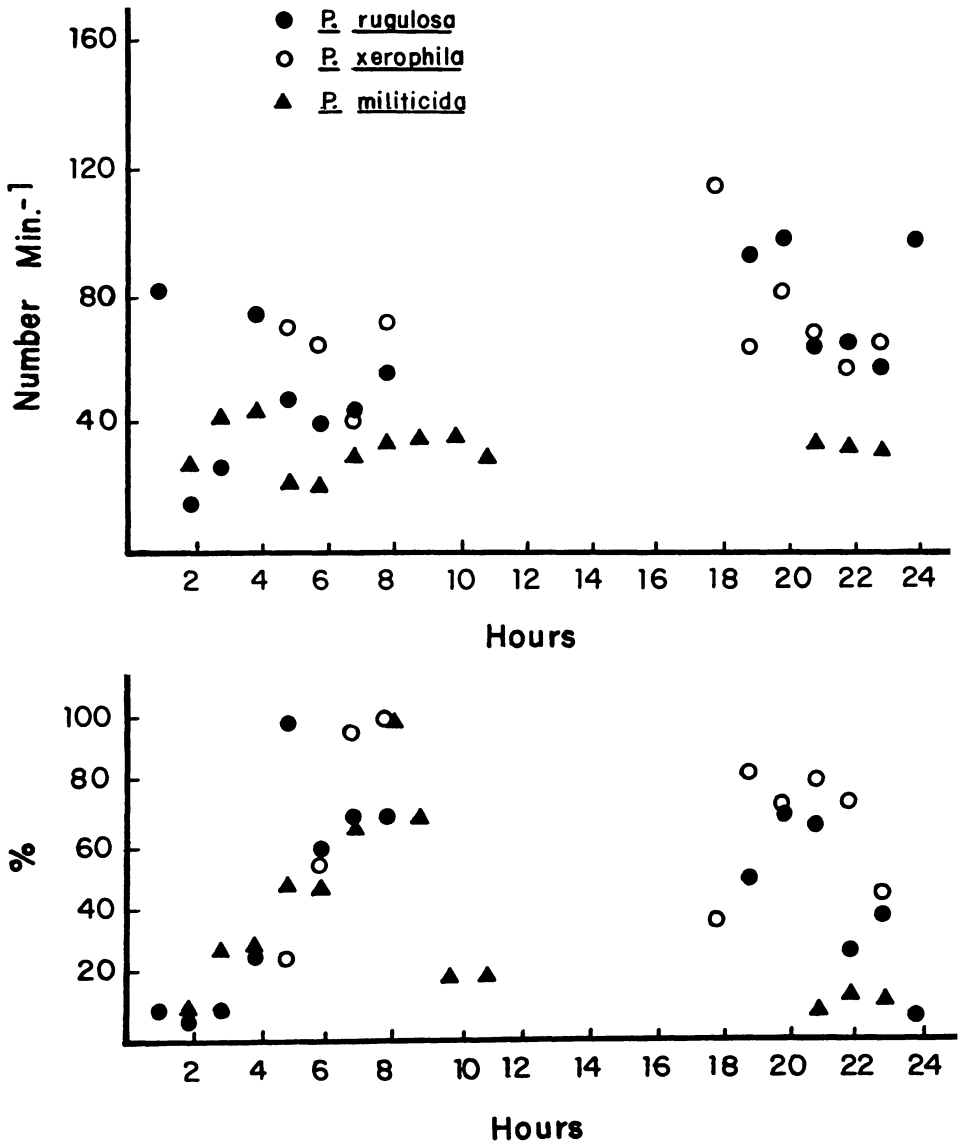


Fig. 1.—Average daily variation in foraging intensity (upper figure) and average daily variation in percent of colonies active (lower figure) in three species of *Pheidole*. The data are a compilation from all habitats studied

accounted for less than 50% of the variance in *Pheidole militica*. The physical environment accounted for only 12-13% of the variance in the dependent variables. In *Ph. rugulosa*, the analysis accounted for 42.5% and 34% of the variance. There was heavy loading on the evaporation variable and lesser loadings on temperature variables and time of day.

In *Pheidole xerophila*, the analysis was similar to that of *Ph. rugulosa* except for important loadings on "rainfall to date" indicating that *Ph. xerophila* responded more quickly to the onset of rains than the other species and to maximum air temperature, indicating that *Ph. xerophila* forages intensively at higher temperatures than the other species.

In August 1975 the estimated density of forbs and grasses in the mesquite-mormon tea community was  $240,088 \cdot \text{ha}^{-1}$ , comprising three grass species and nine species of forbs. Fluff grass *Erioneuron pulchellum* (HBK) Tateoka, at a density of  $73,873 \cdot \text{ha}^{-1}$ , accounted for 94% of the grasses. Buckwheats, *Eriogonum* spp., at a density of  $46,170 \cdot \text{ha}^{-1}$ , accounted for more than 90% of the forbs collected by species of *Pheidole*. In the grama grassland, the annual grama, *Bouteloua aristoides* (HBK), which occurred at an estimated density of  $38,929 \cdot \text{ha}^{-1}$ , accounted for 75-80% of the grass seeds collected by species of *Pheidole*. On the bajada and grama grasslands, eight species of annuals varied in density from  $4,866 \cdot \text{ha}^{-1}$  in creosote bush communities to  $173,557 \cdot \text{ha}^{-1}$  in the grama grassland. The species of *Pheidole* collected mostly the seeds of buckwheat, *Eriogonum abertianum* (Torr.) and a composite, *Malacothrix fendleri* (Gray). Forbs made up a greater percentage of the forage of

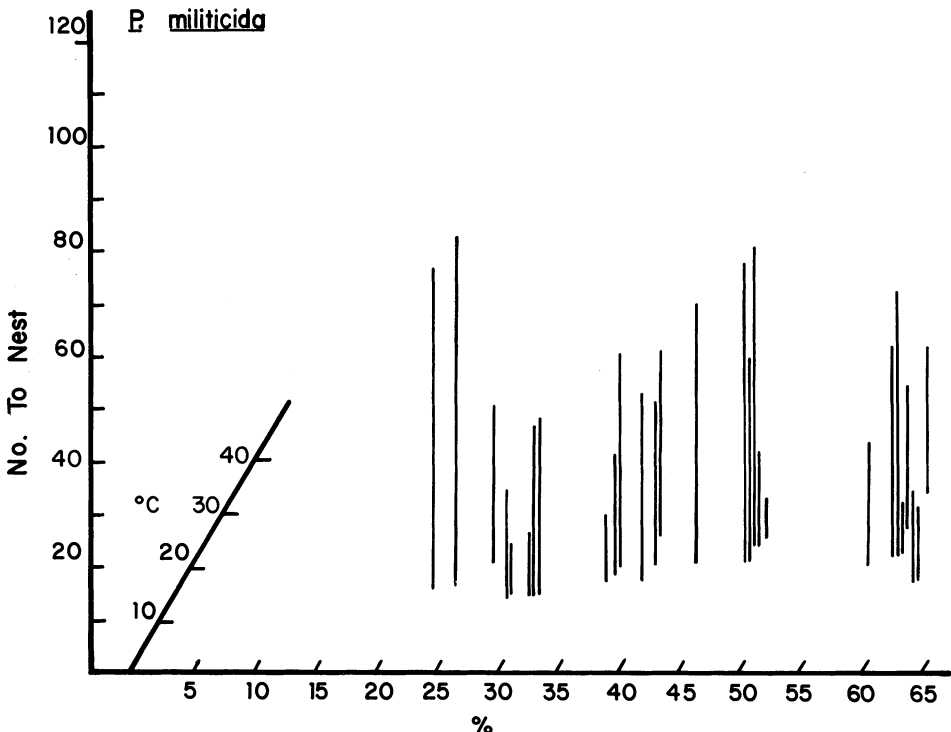


Fig. 2.—The influence of soil surface temperature and air relative humidity on the foraging intensity of *Pheidole militica*

*Ph. militicida* than of *Ph. xerophila* (Table 2). On the bajada *Ph. xerophila* collected a larger percentage of grass seeds than on the playa, and in October and November the forage was almost entirely fluff grass seeds (*E. pulchellum*). *Pheidole militicida* foraged primarily in areas where piles of annual fruits (mostly buckwheats) accumulated as a result of sheet flow water in late summer rains. *Pheidole militicida*

TABLE 2.—Percent composition of forage collected by *Pheidole militicida* and *Ph. xerophila* on the upper watershed (creosote bush and grama grassland communities) and the lower watershed (mesquite-mormon tea community) August-November 1975

	<i>Pheidole militicida</i>		<i>Pheidole xerophila</i>	
	Lower		Upper	Lower
	August - Sept.		August - Sept.	
forbs	86.3		18.5	53.8
grasses	17.6		81.1	30.5
inedible	1.1		0.4	15.8
	October		October	
forbs	48.6		4.5	28.9
grasses	40.4		92.0	71.1
inedible	11.0		3.5	0
	November		November	
forbs	79.2		0	24.9
grasses	18.9		100	70.8
inedible	1.9		0	4.3

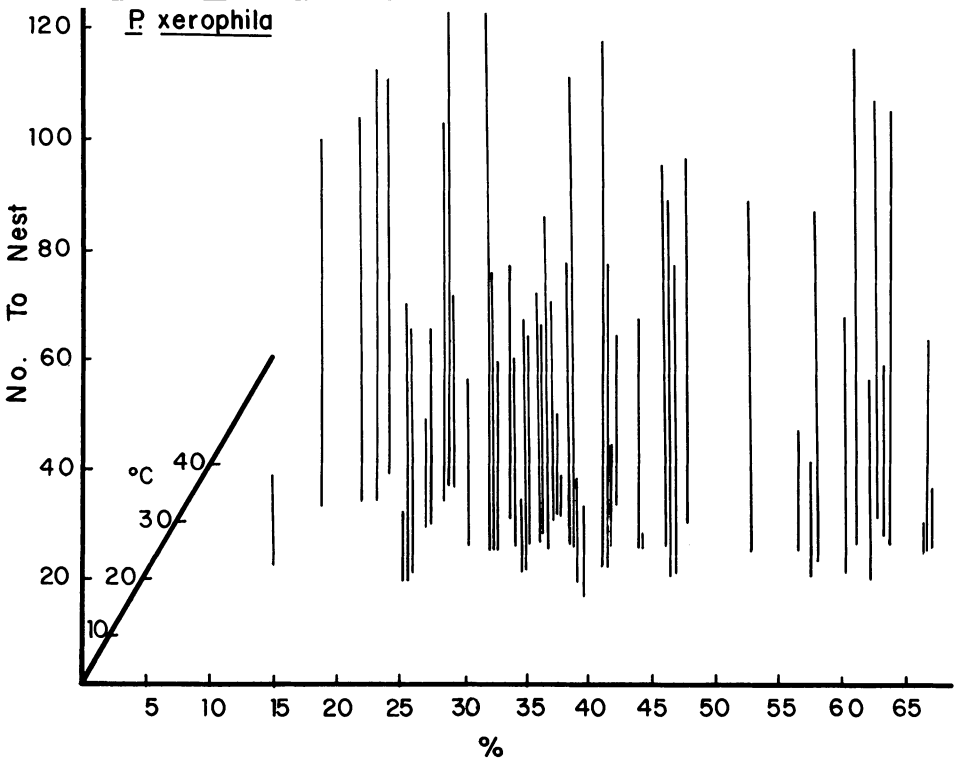


Fig. 3.—The influence of soil surface temperature and air relative humidity on the foraging intensity of *Pheidole xerophila*

foraging columns were several meters long (5-20m) between the nest and an accumulation of seeds. *Pheidole xerophila* and *Ph. rugulosa* columns were shorter (0-6m) and tended to terminate in clumps of grass or forbs where fruits were on the ground.

The percentage of returning foragers carrying forage items in their mandibles varied between 12% and 25.60% (Table 3).

We observed no aggressive behavior between species. On several occasions *Pheidole rugulosa* or *Ph. xerophila* foragers were observed carrying discarded items from the trash dumps of the other species. Both *Ph. rugulosa* and *Ph. xerophila* were foraging at the trash dumps of *Ph. militica*. On four occasions we recorded *Ph. rugulosa* foraging columns crossing foraging columns of *Ph. militica* without aggressive interactions or disruption of trail following in either species.

The occurrence of major workers at the surface appeared to be related to intense foraging activity. Major workers were rarely seen transporting seeds. If major

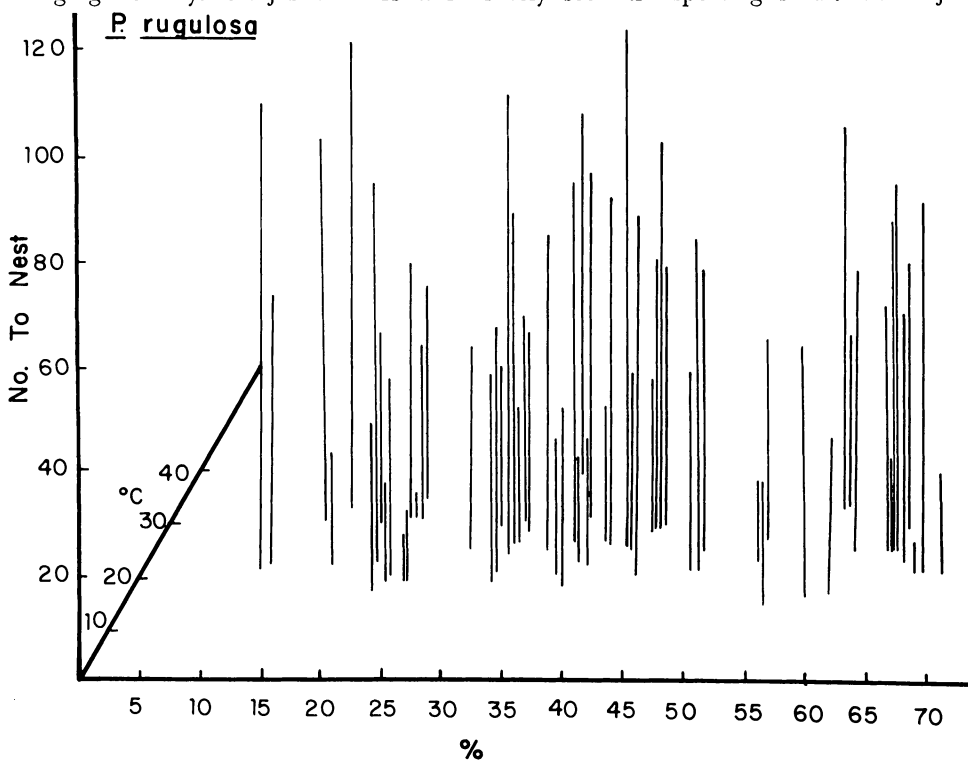


Fig. 4.—The influence of soil surface temperature and air relative humidity on the foraging intensity of *Pheidole rugulosa*

TABLE 3.—The percentage of returning foragers carrying forage items. L and U refer to upper and lower watershed

	Aug.-Sept.	Oct.	Nov.	Dec.
<i>Pheidole militica</i> (L)	23.3	13.8	30	12
<i>Pheidole xerophila</i> (L)	14.7	8.5	25.6	not foraging
<i>Pheidole xerophila</i> (U)	23.2	9.5	20	not foraging

workers wandered more than ca. 20 cm from the nest, several minor workers would drive or carry the major worker back to the nest. In all species more majors were present on the surface following rains. This was especially pronounced in *Pheidole militicida* in which majors were rarely seen on the surface except after rains.

In late October and November, we noted increasing numbers of heads of *Pheidole xerophila* and *Ph. rugulosa* majors in the trash dumps. The number of heads per trash dump varied from 5 - 6 to as many as 30-35 on a given date.

#### DISCUSSION

In Chihuahuan desert ecosystems the large-body-size seed foragers, the species of *Pogonomyrmex*, are primarily diurnal (Whitford and Ettershank, 1975; Whitford, 1978) while the small-body-size *Pheidole* spp. are primarily crepuscular. There is considerable overlap in seed selection in species of both *Pheidole* and *Pogonomyrmex*; both concentrate on buckwheats, *Eriogonum* spp., annual grama grasses and fluff grass (Whitford, 1978, and unpublished field notes on *Pogonomyrmex* in creosote bush communities). Interspecific competition in seed-harvesting ants in these desert communities appears to be avoided more by temporal segregation than by body size/forage size considerations or spatial separation as suggested by Davidson (1977).

*Pheidole* spp. and *Pogonomyrmex* spp. segregate not only on the basis of diurnal activity but also seasonally. *Pogonomyrmex* spp. exhibit peak activity in early and midsummer; from mid-September through November not only are the number of active colonies reduced but foraging intensity is also markedly reduced. *Pheidole rugulosa* and *Ph. xerophila* and *Ph. militicida* maintained increased foraging intensity in October and early November. *Erioneuron pulchellum*, in which seeds mature in late September and early October, was heavily utilized by *Ph. xerophila* and *Ph. rugulosa* (as evidenced by trash piles), with *Pogonomyrmex* spp. virtually absent.

As with the species of *Pogonomyrmex* (Whitford and Ettershank, 1975), it was not possible to predict foraging intensity in species of *Pheidole* by considering characteristics of the physical and biological environment. Factors such as soil surface temperature, moisture content of the air and seed availability (seasonality) explain around 50% of the variation in foraging activity and intensity. The remainder of the variance is probably attributable to the intrinsic behavioral characteristics of the *Pheidole* societies. Factors such as brood development, quantity of seeds in storage and success of scout foragers undoubtedly affect foraging activity. However, such characteristics are extremely difficult to quantify to include in a multivariate analysis.

Since the *Pheidole* spp. switch to diurnal activity in the autumn, temperature is obviously an important off-on switch for activity, and time of day is obviously of little importance except as it reflects suitable temperatures for foraging. Although the CTMax of the species *Pheidole* studied is 46 C, they cease foraging at soil surface temperatures of 35 C whereas *Pogonomyrmex* spp. with CTMax of approximately 55 C continue foraging at soil surface temperatures of 55-60 C (Whitford and Ettershank, 1975). *Pheidole* spp. should be capable of extending their foraging activity to overlap with the activity of *Pogonomyrmex*. This lack of overlap in activity we attribute to the evolution of avoidance of competition by temporal niche reduction.

Only a small percentage (ca. 20%) of returning foragers carried visible forage in their mandibles. A variable portion of the workers of *Pogonomyrmex* spp. also return to the nest without visible forage (Whitford, 1978). We hypothesize that workers returning without forage may simply have eaten and become satiated at a food source, thus reducing the drive to locate suitable forage to return to the nest, or alternatively did not find suitable forage within a suitable period of time. This characteristic of seed-harvesting ants requires further investigation.

The major workers of *Pheidole* appear to serve as seed huskers, removing the



inedible portions of the fruits from the seeds. The inedible portions are then deposited in refuse heaps. Major workers do not forage and surface activity appeared to consist of aimless wandering in the vicinity of the nest crater. The appearance of severed heads of major workers in refuse heaps late in the autumn suggests that these workers may be eliminated from the colony prior to the nonproductive season, hence eliminating them as a drain on food supplies. In drought years this could represent significant energetic savings to *Pheidole* colonies.

*Pheidole* spp. seed removal was estimated by utilizing the data on foraging activity, and estimated numbers of active colonies. Utilizing these data, we obtained the following estimates of seed removal by the *Pheidole* spp. during 1975: creosote bush communities —  $3.44 \times 10^8$  seeds $\cdot$ ha $^{-1}$ ; mesquite-mormon tea community  $3.11 \times 10^8$  seeds $\cdot$ ha $^{-1}$ , and  $9.7 \times 10^8$  seeds $\cdot$ ha $^{-1}$  in the grama grassland. Comparing these estimates with those reported by Whitford (1978) for seed removal by *Pogonomyrmex* in 1 year— $7.3 \times 10^7$  seed $\cdot$ ha $^{-1}$ —*Pheidole* spp. remove nearly 10 times more seeds than do *Pogonomyrmex* spp. in the same habitat. However, since the *Pheidole* spp. collect large quantities of seeds of the perennial fluff grass *Erioneuron pullchellum*, their effect on the composition of the annual plant community is probably not any greater than that of *Pogonomyrmex* spp.

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