# Factors Affecting Foraging Activity in Chihuahuan Desert Harvester Ants[1]

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## ABSTRACT

The foraging activity of 4 species of harvester ants as affected by soil surface temperature, saturation deficit at the soil surface, light and forage availability was studied in a desert grassland area 40 km NNE of Las Cruces, N.M. *Pogonomyrmex* sp. were capable of locomotor activity at temperatures between ca. 5° and 53°C and *Novomessor cockerelli* between 4° and 52°C. *Pogonomyrmex* sp. exhibited maximum foraging intensity at 45°C and *N. cockerelli* at 20°C. Forager population sizes varied among species: 1000–6000 in *P. rugosus,* ca. 1000 in *P. californicus* and *N. cockerelli;* and ca. 200–600 in *P. desertorum. P. rugosus* exhibited peak foraging activity and had the greatest number of colonies active following drought periods, ceasing foraging when granaries were filled, and foraged at night during midsummer. *P. desertorum* and *P. californicus* were strictly diurnal and did not exhibit hoarding behavior. *P. desertorum* responded to soil wetting by shifting activity between watered and unwatered controls directly in response to differences in soil surface temperature. Soil wetting stimulated intense activity in *P. rugosus* at a time when controls were inactive. Foraging in harvester ants seemed to be primarily affected by forage availability, secondarily by microclimate, with historical factors and interspecific competition as contributing parameters in some species.

Harvester ants of the genera *Pogonomyrmex* (Mayr) and *Novomessor* (Emery) are important elements of the Chihuahuan desert arthropod fauna. These ants occur at high colony densities (Schumacher and Whitford 1975), forage primarily on seeds, and are often considered potentially detrimental to range grasses (Race 1966, Lavigne 1966, Cole 1932). Knowledge of the factors which affect foraging activity in these species is an essential first step in evaluating the importance of these arthropods in desert ecosystems.

Most studies dealing with the foraging behavior of harvester ants have been limited to short time spans and/or have evaluated only 1 or 2 factors such as temperature, circadian periodicity, or light (Rogers 1974, McCluskey 1963, Tevis 1958, Bernstein 1974, Creighton 1953, Eddy unpubl.[3], Cole 1934). Bernstein (1974), studying harvester ants along an altitudinal gradient, suggested that foraging activity was correlated with the season of seed production but provided no quantitative data to document this hypothesis.

Because of the unpredictable nature of desert climate and, hence, plant and seed production, studies of the foraging activity of animals dependent on seeds should encompass several years, which could provide a broad spectrum of climatic conditions on which generalizations could be based. Our studies were designed to evaluate seasonal patterns, responses to rainfall, temperature, saturation deficits, and forage availability as factors affecting foraging activity in 4 species of harvester ants.

## Study Area and Description

Our studies centered around 4 sympatric species of harvester ants which are abundant at the Jornada Validation Site and widely distributed in desert areas in the U.S. and Mexico: *Pogonomyrmex rugosus* (Emery), *P. desertorum* (Wheeler), *P. californicus* (Buckley), and *Novomessor cockerelli* (E. Andre). Field studies were conducted on areas adjacent to the Jornada Validation Site, 40 km NNE of Las Cruces, Doña Ana County, N.M.

The Jornada Validation Sites are located on a desert watershed which drains into a small dry lake (playa). The watershed varies in elevation from ca. 2000 to 1000 m. The 50-year average precipitation for the area is 225 mm/year with peak rainfall during July and August (Houghton 1972). Summer maximum temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station). These climatic conditions and topography produce a typical Chihuahuan desert watershed.

Most studies were conducted on a 4-ha plot characterized by a sandy loam with a hard-pan, calcium carbonate deposition layer (caliche) at ca. 100 cm. The dominant plants and their densities on the area are honey mesquite, *Prosopis glandulosa juliflora,* 280/ha; mormon tea, *Ephedra trifurca,* 403/ha; snakeweed, *Xanthocephalum sarothrae,* 494/ha; creosotebush, *Larrea tridentata,* 97/ha; and soap tree yucca, *Yucca elata,* 131/ha (Whitford and Ludwig, 1971). Some studies were conducted on an area ca. 0.9 km from the primary study site. This area had sandy soils with considerable gravel and scattered *Larrea tridentata* and *Ephedra trifurca.*

## Methods

Foraging activity was studied by placing a wire reference circle (0.5 m radius) over 5 to 15 randomly selected nests of harvester ants. The circles were divided into 8 equal segments. Activity was monitored by counting the number of ants returning

to a nest per unit time. Frequently the numbers of ants returning to the nest were too great to count accurately. When this occurred, the numbers crossing a segment (⅛–½) of the reference circle were counted. When several segments were counted at a single measurement period, they were selected at random to eliminate the bias of a segment over a foraging trail. Foraging activity was calculated by multiplying the number of ants returning by the denominator of the reference circle fractions, and dividing by the number of minutes observed. At each observation period, wet and dry bulb air temperatures were measured adjacent to a nest as close to the soil-air interface as possible with a gun psychrometer or sling psychrometer. The relative humidity was converted to saturation deficit (g $H_2O/m^3$ air). Soil surface temperature was obtained by laying the bulb of a mercury thermometer on the soil surface and covering it with a fine layer of sand. Foraging activity was monitored at 2-h intervals from dawn until dusk once a week or every 2 wk, depending on the season. Several all-night activity studies were conducted in midsummer when foraging in some species did not cease at sunset. Observations were made with portable fluorescent lamps. Preliminary studies with lights with colored filters showed that light had no measurable effect on the activities of the species studied.

We monitored foraging activity on areas which had been watered for comparison with data obtained under natural conditions. Areas around 4 *P. desertorum* colonies and 2 *P. rugosus* colonies (ca. 50 m in diameter) received between 2400 to 4000 liters. Water was applied as evenly and as rapidly as possible with pooling. Watering was alternated from one nest to another over a 3 to 4-h period. Watering was performed between 2–4 h before sunset and observations were made during the next day on watered and unwatered plots. The water regime produced noticeable wetting to a depth of 10–15 cm.

Seed production of grasses and forbs was estimated by harvesting plots (perennial grasses) and by harvesting plants encountered in estimating density by the point-quarter method (Phillips 1959). Biomass of reproductive structures reported in this study represent estimated standing crop at the end of a growth period (Fig. 5). In the Chihuahuan desert, peak seed production of different species groups of grasses and forbs may occur in May, July and/or September depending on the rainfall pattern.

Densities of active colonies of harvester ants were estimated monthly by the point-quarter method (Phillips 1959). A total of 40 randomly placed stakes were used as center points and the distance to the nearest active colony of harvester ants in each of the 4 quadrants was measured. Density was calculated from average distance and numbers of colonies.

Determination of lethal temperatures in arthropods requires considerable time and large samples. In an assessment of foraging behavior, that temperature at which insects are immobilized is much more useful in an assessment of factors affecting foraging.

Critical thermal maxima and minima are defined as the statistical mean of the temperatures at which individual animals are immobilized by temperature and, thus, incapable of escaping conditions which will lead to death. CTMax was measured by placing groups of 4–5 ants in a flask containing a layer of sand on the bottom. The flask was seated in a heating mantle and the temperature ca. 2–3 mm above the surface raised at a rate of 1°C/min using a variable transformer. CTMin was measured in a similar container which was cooled by circulating coolant through coils around the container. The cooling rate of 0.5°C/min was regulated by regulating flow. Temperatures were measured using a thermistor mounted 2–3 cm above the sand surface and read on a Yellow Springs Instrument Telethemometer.

Estimates of forager populations were made by the Lincoln Index. Foragers were collected with an aspirator as they returned to the nest. Precensus and census numbers captured varied between 100–200 in *P. rugosus*, and between 30 and 100 in *P. californicus* and *P. desertorum*, depending on the activity of the colony. The ants were immobilized by placing the aspirator jar in an ice-filled container. Immobilized ants were marked with a dot of airplane dope (paint) on the gaster. Colonies had to be censused within 48 h since ant grooming tends to eliminate these marks (Brian 1971).

## Results

Seasonal and daily activity are directly affected by temperature since temperatures lower than the minimum for mobility preclude activity as do temperatures approaching the upper lethal limit. The CTMax and CTMin for the species studied are presented in the following table:

| Species | CTMax | CTMin |
|---|---|---|
| *Pogonomyrmex californicus* | 52.9±0.58 | 4.66±1.89 |
| *Pogonomyrmex desertorum* | 53.2±0.66 | No data |
| *Pogonomyrmex rugosus* | 53.8±0.52 | 4.77±1.76 |
| *Novomessor cockerelli* | 51.7±1.72 | 3.64±1.75 |

Temperatures of ca. 5°C represent the lower threshold for locomotor activity in most of these species and temperatures between 50°C and 55°C represent the upper maximum. Seasonal fluctuations in soil-surface temperatures and soil temperatures at 15 cm depth at the study area are presented in Fig. 1. In spring and fall, these conditions would typify most Chihuahuan desert areas between 1000 and 1300 m elevation, allowing for fluctuations due to soil characteristics and latitude. Initiation of activity in the spring and cessation in the fall is dependent on the temperature of the upper nest chambers at ca. 15 cm depth, where some foragers overwinter. These foragers are capable of emerging when temperatures exceed 5°C. Field observations (Table 1) support the contention that the physiological minimum temperatures for activity must be exceeded before activity can be initiated. No activity was noted during December and January when soil temperatures at 15 cm were less than 5°C. Conditions in December and
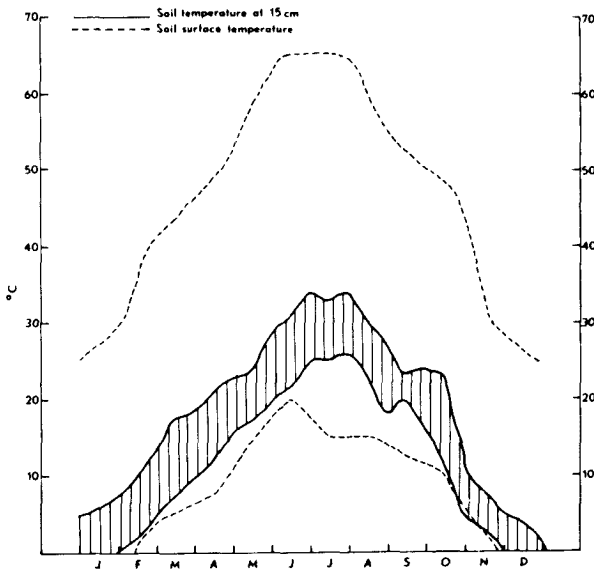
FIG. 1.—Seasonal fluctuations in soil temperature at 15 cm depth and soil surface temperatures at the Jornada Site during 1972.

January resulting in soil temperatures greater than 5°C were so infrequent that the data on active colonies were not included in Table 1.

Although physiological temperature tolerance sets limits on time available for foraging in harvester ants, the harvester ant community does not utilize the entire spectrum of conditions available to it. Midsummer foraging in response to soil-surface temperatures and saturation deficits is shown in Fig. 2. *Novomessor cockerelli* exhibited peak activity at 20°C and all 3 *Pogonomyrmex* spp. exhibited peak foraging activity at 45°C. Some *P. californicus* were active at soil-surface temperatures above the CTMax.

Activity under these conditions, i.e. > 60°C, was limited to short forays across the hot surface followed by ascent into plants several centimeters above the surface where the microclimatic temperatures varied between 35–45°C. These short bursts of activity on the hot soil surface were obviously of insufficient length to allow the ant's body temperature to reach CTMax.

Because of the relationship between soil-surface temperature and saturation deficit, it was not possible to assess the relative importance of these factors as regulators of foraging activity. Using a bi-quadratic multiple regression of the form $y = B_0 + B_1X_1^2 + B_2X_2^2 + B_3X_2 + B_4X_2 + B_5X_1X_2$, where $y$ = foraging activity, $X_1$ = soil-surface temperature and $X_2$ = saturation deficit, we found that these variables only accounted for 10–40% of the variation in foraging activity ($r^2$ between 0.11 and 0.49) in all species studied. Unfortunately, it is not possible to separate the effects of temperatures and saturation deficit since water-holding capacity of the air and, hence, saturation deficit increases with increased temperature.

In all 4 years of the study, *N. cockerelli* foraged diurnally from February through early May and from mid-September through November. In midsummer, *N. cockerelli* was mainly nocturnal, initiating activity 2–3 h prior to sunset and continuing activity 2–3 h after sunrise.

In all of the species studied, rainfall stimulated activity (Schumacher and Whitford 1975). The intensity of this activity and type of activity, i.e., foraging, nest-disc repair, or nest cleaning, depended on season, forage availability, and previous history, as will be discussed in a later section.

In June 1973, there was no nocturnal foraging in *P. rugosus* at soil-surface temperatures and saturation deficits noted during intense foraging activity in early July and during some nocturnal foraging occur-

Table 1.—Percent of maximum number of colonies active in *Pogonomyrmex californicus*, *P. desertorum*, *P. rugosus* and *Novomessor cockerelli*. ND indicates missing data. + indicates active colonies recorded in other localities on dates other than census dates. Data reflect diel activity only. Maximum density (MD) in numbers of colonies per hectare did not differ significantly between years.

| | MD | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **1972** | | | | | | | | | | | |
| P. californicus | 45 | + | + | + | + | 15 | 30 | 60 | 100 | 80 | 30 |
| P. desertorum | 138 | + | + | + | 3 | 30 | 100 | 100 | 80 | 5 | 0 |
| P. rugosus | 21 | + | + | + | 60 | 100 | 100 | 70 | 20 | 0 | 0 |
| N. cockerelli | 18 | + | + | 33 | 15 | 75 | 100 | 100 | 51 | ND | 66 |
| **1973** | | | | | | | | | | | |
| P. californicus | | 11 | 55 | 100 | 50 | 22 | 70 | 45 | 77 | 45 | 45 |
| P. desertorum | | 2 | 0 | 2 | 28 | 43 | 60 | 100 | 30 | 2 | 0 |
| P. rugosus | | 40 | 10 | 30 | 0 | 0 | 100 | 30 | 20 | 0 | 0 |
| N. cockerelli | | + | 40 | 0 | 0 | 0 | 40 | 20 | 20 | 100 | 0 |
| **1974** | | | | | | | | | | | |
| P. californicus | | + | + | 5 | 21 | 25 | 31 | 86 | ND | 100 | ND |
| P. desertorum | ND | + | 5 | 5 | 0 | 18 | 52 | 61 | ND | 100 | ND |
| P. rugosus | | + | + | 5 | 4 | 13 | 50 | 42 | ND | 100 | ND |
| N. cockerelli | | + | + | 0 | 0 | 18 | 100 | 100 | ND | 62 | ND |
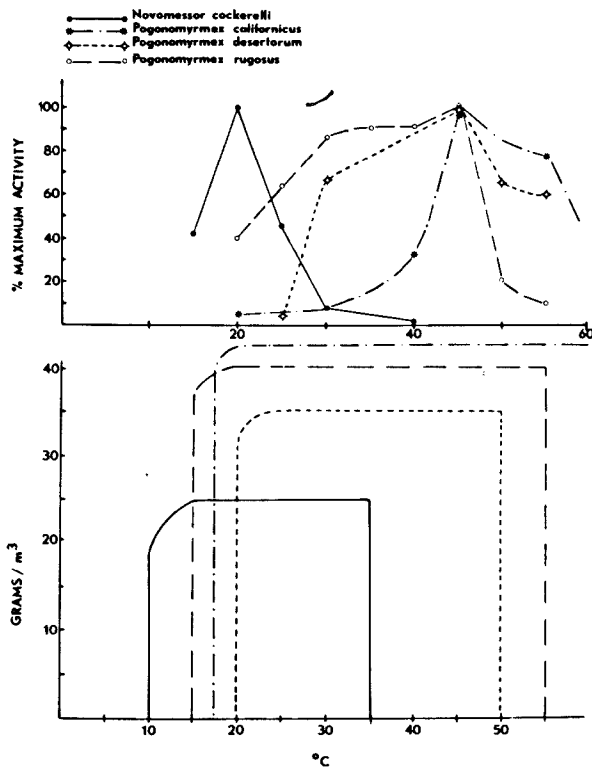
FIG. 2.—Effects of temperature and saturation deficits on the activities of 4 species of harvester ants. Upper: relationship between the percent of maximum foraging activity (actual numbers of ants returning to the colony/min divided by the max. no. of returning foragers/min). Foraging activity was calculated as mean activity for 5–10 colonies, depending on species. Lower: range of temperatures and saturation deficits measured as close to the soil surface as possible over which foraging activity in each species was measured in the field. The areas under the curve indicate the temperature-saturation deficit environments used by the individual species.

ring in May (Table 2). Nocturnal foraging in *P. rugosus* during July was greatest immediately after sundown then decreased gradually as nighttime soil temperatures dropped.

In midsummer *N. cockerelli* exhibited peak foraging activity in the middle of the night (Table 2). Spring and fall foraging in this species occurred during daylight hours when climatic conditions were favorable. The switch to nocturnal foraging in midsummer was coincident with increased surface activity of termites (Johnson and Whitford 1975) and other arthropods (Whitford 1974).

Estimated numbers of foragers varied among species; it also varied with year and with season (Table 3). *P. rugosus* colonies had the largest number of foragers and greatest variation among colonies with estimates ranging from 1000–6000 during the month of peak foraging activity. However, the average numbers of foragers per colony (ca. 1000) was similar in *P. rugosus*, *P. californicus*, and *N. cockerelli*. In 1972, all species actively foraged throughout the summer but we concentrated our efforts on *N. cockerelli* and *P. rugosus*. In 1973, relatively few *P.*

Table 2.—Average nocturnal foraging activity (numbers of ants returning/min) in 10 colonies of *Pogonomyrmex rugosus* in May, June, and July 1973, and in 5 colonies of *Novomessor cockerelli* in May, June, and July 1972. OD indicates observations discontinued after that hour.

| Hour | May P. rug. | May N. coc. | June P. rug. | June N. coc. | July P. rug. | July N. coc. |
|---|---|---|---|---|---|---|
| 1900 | 15 | 0 | 0 | | | ND |
| 2000 | 11 | 0 | 0 | 2 | 83 | 13 |
| 2100 | 12 | 0 | 0 | 14 | | 11 |
| 2200 | | | | 46 | | 11 |
| 2400 | OD | OD | 0 | OD | 67 | 61 |
| 0200 | | | 0 | | 31 | 11 |
| 0400 | | | 0 | | 22 | 14 |
| 0600 | | | OD | | 0 | 4 |

*rugosus* colonies were active and the active colonies were characterized by lower numbers of foragers than in 1972. *P. desertorum* colonies had smaller numbers of foragers than the other 3 species but its colony densities (138/ha) were 6.5 times greater than *P. rugosus* and 3.5 times greater than *P. californicus*.

Forager numbers were lower in spring and early summer than they were in midsummer in all of the species studied. In 1972, callow workers of *P. rugosus* and *P. californicus* were recruited into the

Table 3.—Forager population numbers ± the standard error of the estimate in 4 species of harvester ants. Population estimates were obtained by mark-recapture and calculated by the Lincoln Index. Most data are for 1972; 1973 data indicated by *.

| Month | Novomessor cockerelli | Pogonomyrmex californicus | Pogonomyrmex desertorum | Pogonomyrmex rugosus |
|---|---|---|---|---|
| April–June | 250± 31 | | 158± 55 | 3333±1895 |
| | 429±152 | | *210± 84 | 630± 129 |
| | | | *152± 34 | 217± 31 |
| | | | *168± 42 | 218± 27 |
| | | | *258±140 | |
| June | 606±138 | 337± 157 | 260±141 | 217± 136 |
| | 400± 69 | 613± 293 | 184± 48 | 218± 92 |
| | 549±112 | | 227± 84 | 824± 211 |
| | 557±123 | | *133± 39 | *431± 143 |
| July | 1391±297 | 557± 315 | *913±330 | 1044± 129 |
| | 1836±389 | 1464± 405 | *353±125 | 1464± 404 |
| | 2208±589 | 1103± 573 | *817±455 | 6063± 130 |
| | | 3091± 315 | *439±138 | *645± 176 |
| | | 3829± 731 | *506±212 | |
| | | *107± 22 | *246± 68 | |
| | | *130± 52 | *409±135 | |
| | | | *202± 29 | |
| August | 585±133 | 1011± 153 | 284± 65 | 1519± 248 |
| | 762±199 | 2881±1989 | | 548± 48 |
| | 1342±262 | | | 758± 93 |
| | 1650±334 | | | 734± 112 |
| | 1884±527 | | | 496± 74 |
| | | | | 479± 55 |
| | | | | 818± 83 |

forager population during July. Two colonies of *P. rugosus* which were excavated in August 1972 had a total of 1595 workers and 180 pupae, and 2195 workers and 180 pupae, respectively. A *P. californicus* colony excavated in September yielded 1932 workers and no pupae. A *P. rugosus* colony excavated Sept. 15, 1973, yielded 3639 workers and 321 pupae.

The effects of evening watering on foraging activity the following day are summarized in Fig. 3 and 4. In 4 experiments on *P. rugosus* in June and July 1973, the average number of workers returning to the nest was 116/min. Concommitant soil temperatures and saturation deficits (Sat D) around the experimental colonies varied from 20°C and 6 g/m³ at 0730 h to 54°C and 40 g/m³ at 1330 h. Around the controls, $T_s$ and Sat D varied from 25°C and 8 g/m³ at 0730 h to 61°C and 43 g/m³ at 1430 h, and the average number of foragers returning to the colony was 0.05/min.

The response of both experimental and control *P. desertorum* was one of continuous increase in activity
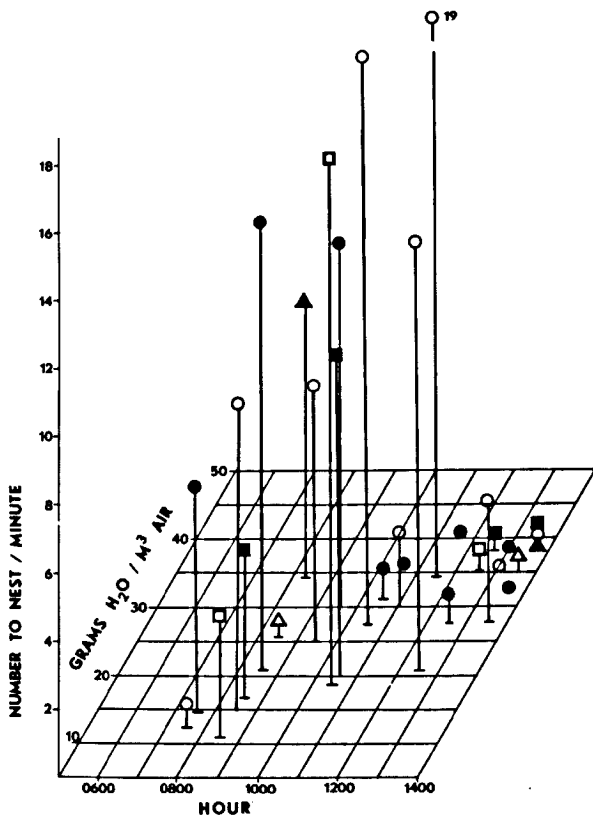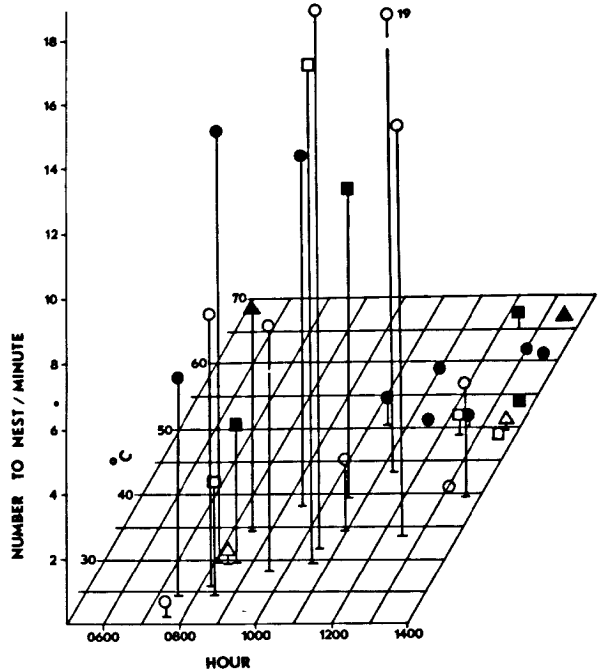


FIG. 4.—Effects of water amendment on foraging intensity of *Pogonomyrmex desertorum* as affected by soil-surface temperature. Method of presentation same as Fig. 3.

until $T_s$ reached ca. 45°C, then activity gradually decreased (Fig. 3 and 4). In the early morning, experimental colonies experienced lower $T_s$ than controls and the controls exhibited higher activity. This situation reversed as the $T_s$ and Sat D of controls reached high levels sooner than the experimental areas.

In one set of experiments, 3 colonies of *P. desertorum* received < ½ the water applied to the other 2 nests of this species. Although there were no differences in $T_s$ and Sat D (49°C and 36 g/m³ at 1500 h), the colonies which received heavy watering were active ($\bar{x}$ = 3.5/min) while activity was absent in the other 2 colonies.

Although immediate climatic factors affect foraging and other activities, the activity of desert harvester ants is affected to a large extent by an historical component. Not all colonies were active all months of each year during favorable conditions. Yearly differences in foraging activity measured as the maximum number of foragers returning to the nest per minute in *Pogonomyrmex* spp. are shown in the following table. Data in parentheses indicate numbers foraging at night prior to midnight.



FIG. 3.—Effects of water amendment on the foraging intensity of *Pogonomyrmex desertorum* as affected by saturation deficit (g $H_2O/m^3$ air). Data for watered plots are open symbols. Data for controls are solid symbols. Data from different dates are shown by different symbols. Activity (number of foragers returning to the nest/min) is indicated by height of symbol above the plane. Paired observations are indicated by open and solid symbols at the same hour.

| Date | P. rugosus | P. californicus | P. desertorum |
|---|---|---|---|
| 1971 | 2.5 | No data | No data |
| 1972 | 100 (68) | 18 | 12 |
| 1973 | 1.3 (83) | 18 | 19 |

Foraging activity measured in the present study was largely correlated with seed production and avail-
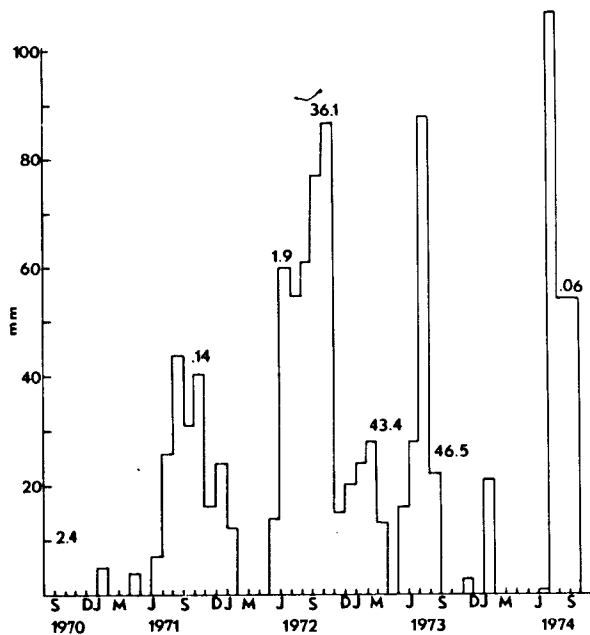
FIG. 5.—Rainfall during the period of study. The numbers above the bars are biomass of reproductive structures of forbs and grasses in kg/ha and indicate peak standing crop at the time indicated.

ability of seeds of forbs and grasses on the soil surface. Rainfall and seed production during the period of this study are presented in Fig. 5. *P. desertorum* exhibited a midsummer peak in 1972 and 1973, but a late summer peak in 1974. In 1972 and 1973 more *P. californicus* colonies were active in spring and fall than in midsummer. In the drought year (1974) the maximum numbers of colonies of all *Pogonomyrmex* spp. were active in the fall (Table 1).

The importance of historical climatic events as regulators of foraging activity in desert harvester ants is further documented in Table 3 and data on differences in foraging rates presented above. *P. rugosus* responded to drought conditions and limited diversity of seed resources by sending out relatively few foragers per unit time. Monthly hours suitable for foraging were estimated from climatic conditions and are presented in the following table:

| Date | *P. rugosus* | *P. californicus* | *P. desertorum* |
|---|---|---|---|
| 1971 | 27 | 60 | 21 |
| 1972 | 85 | 34 | 65 |
| 1973 | 20 | 34 | 65 |
| 1974 | 27 | 60 | 21 |

In 1972, the foraging activity was 40 times greater than the drought year, but the following year *P. rugosus* virtually ceased foraging during the day, although density and species diversity of annual plants was as high as the previous year (Whitford 1973, 1974). The same historical component is noted in the percent of month hours actually used in foraging by the various species of *Pogonomyrmex*.

## Discussion

Analysis of factors affecting foraging activity in desert harvester ants is complicated because of the importance of seasonal and historical parameters. Rogers (1974) developed regression equations for *P. occidentalis* predicting numbers of foraging ants leaving the colony relative to surface temperatures. His studies were limited to one year, June through September 1970, and to a single colony for a 3-day period in 1971. Since *P. occidentalis* lives in an environment where seed production is more predictable than do desert *Pogonomyrmex* species, Roger's equations may not be appropriate to the complex of components and unreliability of abiotic factors affecting activity of such species.

Bernstein (1974) stated that environmental cues regulate foraging times and suggested soil-surface temperature and light intensity as important cues. Her studies of ant species along an altitudinal gradient suggested that foraging schedules in seed-harvesting ants were more likely adaptations to seasonal production of food rather than to daily events. Unfortunately, this conclusion was not well documented. The studies of Rogers (1974) and Bernstein (1974) contain insufficient data to provide an understanding of factors affecting foraging in desert harvester ants.

Data presented in this study do contribute to an understanding of the foraging strategies of desert harvester ants. *Novomessor cockerelli* should be considered separately because it forages as a generalist and is much more dependent on insects than are the harvesters of the genus *Pogonomyrmex* (Whitford, unpubl. data). We propose that changes in intensity of nocturnal foraging in *N. cockerelli* are coincident with activity of preferred arthropod prey species, but we lack documentation of this hypothesis. In spring and fall, *N. cockerelli* was a diurnal forager. The switch to nocturnal foraging occurred when soil-surface temperatures during most of the day exceeded 30°C and when night air and soil-surface temperatures remained above 15°C. Even in midsummer *N. cockerelli* foraged at midday following rains or when overcast conditions modified the environment at the soil surface. Thus, nocturnality in this species is facultative, allowing escape from harsh environmental conditions. Although *N. cockerelli* did not appear to be as dependent on the availability of the seeds of forbs and grasses as were *Pogonomyrmex* species, variation in seasonal activity in numbers of colonies actively foraging, numbers of foragers per colony, and foraging intensity from year to year paralleled that of the *Pogonomyrmex* species.

*Pogonomyrmex* species differ in seasonality of maximum number of active colonies as well as in response to daily environmental conditions. The most obvious relationships documented by this study are those between forage availability and foraging effort. The differences in diel, seasonal, and yearly patterns of colony activity represent differing strategies used to exploit a common resource: seeds.

In *P. rugosus* the most important regulators of foraging activity are (1) the degree of colony satiation, and (2) the availability of suitable forage. Evidence for the importance of colony satiation, while indirect, is convincing. Although there was an abundance of annual forb and grass seeds in both 1972 and 1973, *P. rugosus* virtually ceased activity during 1973, exhibiting peak numbers of active colonies and peak foraging activity only in 1972 which followed a drought year, 1971, in which there was an essential absence of forb- and grass-seed production. In studies of foraging territories in *P. rugosus* (Whitford 1975) it was found that several colonies were "uncooperative after our initial tests." These colonies were invariably the most active during the initial trials, then ceased foraging after one or two days. When the surface granaries of these colonies were opened they were filled with the dyed seeds used in the experiments. These data tend to support the contention that when the granaries of *P. rugosus* are full, foraging is curtailed even though seeds are abundant.

The absence of diurnal foraging but presence of intense nocturnal foraging in the summer of 1973 was probably associated with predation in *Pogonomyrmex* species on termites and other insects. The gathering of insects at night provides the colonies with a high-quality protein source not readily available in seeds. The reduced amount of diurnal foraging in 1973 appears to have been maintained at a level necessary to replace seeds consumed with no apparent effort to build up additional stores.

Responses to availability of suitable forage are more difficult to document but our studies do provide some data that support the importance of this variable. In early summer, 1972, numbers of active colonies and foraging intensity were low, although granary reserves had undoubtedly been depleted during the 1971 drought.

The increases of forager numbers during midsummer coincident with peak forage availability and the recruitment of callow workers into the forager population in *P. rugosus* provide additional evidence that forage availability is an important regulator of foraging activity in *Pogonomyrmex*. The increase of forager numbers can be attributed to 2 factors: (1) increased availability of seeds resulting in greater recruitment of foragers, and (2) addition of workers to forager populations due to reproductive activity in late spring and early summer. The peaking of forager numbers coincident with peak forage occurred in all species studied. Thus, it would appear that the increase in forager population size in midsummer may simply be an expression of reproduction in the colony.

Forage activity patterns in *P. desertorum* and *P. californicus* were similar in some respects to those of *P. rugosus* and differed primarily in seasonal peaks and diel patterns. During periods of low abundance of seeds on the soil surface in 1971 and 1974, both species were represented by fewer active colonies in spring and early summer than were recorded during

the years of high seed production. Hence, colony response to seed availability appears to be somewhat similar to that of *P. rugosus*.

Seasonal and diel differences in foraging activity between *P. californicus* and *P. desertorum* may result from interspecific competitive interactions, documentation of which are beyond the scope of this paper. Since both species are of a similar size, prefer the same seeds, and have essentially the same physiological activity limits, interspecific competition undoubtedly accounts for most differences between these species. Neither species is a nocturnal forager and both share with *P. rugosus* an optimum temperature of 45°C for maximum foraging activity. Forage availability appears the best predictor of their activity.

### Acknowledgment

### REFERENCES CITED

Bernstein, R. Z. 1974. Seasonal food abundance and foraging activity in some desert ants. Am. Nat. 108: 490–8.

Brian, M. V. 1971. Ants and termites. Pages 247–61 in J. Phillipson, ed. Methods of study in quantitative soil ecology: population production and energy flow (IBP Handbook no. 18). Blackwell Scientific Publ., Oxford.

Cole, A. C. 1932. The relation of the ant, *Pogonomyrmex occidentalis* Cresson, to its habitat. Ohio J. Sci. 32: 133–46.

_____ 1934. An ecological study of the ants of the southern desert shrub region of the United States. Ann. Entomol. Soc. Am. 27: 388–405.

Creighton, W. S. 1953. New data on the habits of the ants of the genus *Veromessor*. Am. Mus. Novit. 1612: 1–18.

Houghton, F. E. 1972. Climatic guide, New Mexico State University, Las Cruces, New Mexico, 1851–1971. N.M. Agric. Exp. Stn. Res. Rpt. 230. 20 pp.

Johnson, K. A., and W. G. Whitford. 1975. Foraging ecology and relative importance of subterranean termites in Chihuahuan desert ecosystems. Environ. Entomol. 4: 66–70.

Lavigne, R. J. 1966. Individual mound treatments for control of the western harvester ant, *Pogonomyrmex occidentalis*, in Wyoming. J. Econ. Entomol. 59: 525–32.

McCluskey, E. S. 1963. Rhythms and clocks in harvester and Argentine ants. Physiol. Zool. 36: 273–92.

Phillips, E. A. 1959. Methods of vegetation study. Holt, Rinehart and Winston, Inc., New York. 107 pp.

Race, S. R. 1966. Control of western harvester ants on rangeland. N.M. Agric. Exp. Stn. Bull. 502. 21 pp.

Rogers, L. E. 1974. Foraging activity of the western

harvester ant in the shortgrass plains ecosystem. Environ. Entomol. 3: 420–4.

Schumacher, A. M., and W. G. Whitford. 1975. Spatial and temporal variations in Chihuahuan desert ant faunas. Southwest. Nat. (in press).

Tevis, L., Jr. 1958. Interrelations between the harvester ant, *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39: 695–704.

1973. Jornada validation site report. Desert Biome US/IBP Res. Mem. 73–4. 331 pp.

1974. Jornada validation site report. Ibid., 74–4. 110 pp.

Whitford, W. G. 1975. Foraging behavior of Chihuahuan desert harvester ants. Am. Midl. Nat. (in press).

Whitford, W. G., and J. A. Ludwig. 1971. Validation study: The Jornada validation site (Playa—N.M.S.U. Ranch). Desert Biome US/IBP Rep. 2223: 1–68.