SPATIAL AND TEMPORAL VARIATION IN CHIHUAHUAN DESERT ANT FAUNAS

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ABSTRACT. Estimates of colony densities of active colonies of ants were made at frequent intervals throughout the year in two Chihuahuan desert communities: a creosotebush bajada and mesquite-mormon tea playas fringe community. Densities of harvester ants, *Pogonomyrmex*, were higher on the playa site; and seed harvesters, *Pheidole*, were higher on the bajada. Some ant species exhibited specific habitat requirements with regard to soil type and/or plant cover: *Formica perpilosa*, *Pogonomyrex imbericulus*, *Trachymyrmex smithi neomexicanus*. Other species were more generally distributed. Two congeneric species pairs exhibited differences in seasonal activities suggesting competitive interactions. Peak densities of active ant colonies exceeded 4,000 colonies ha⁻¹ on the playa and 2,000 colonies ha⁻¹ on the bajada.

Studies of North American ant communities have been largely limited to relationships with plant communities (Conklin 1972; Gregg 1973; Wheeler and Wheeler 1973). Most studies in which densities of ant colonies have been estimated have limited their scope to one or two species and to estimates made during mid-summer (Talbot 1943; Rogers et al. 1972). The interpretation of the functional role of an animal community in an ecosystem requires analysis of the spatial and temporal relationships between the species in the community. Therefore, we initiated studies designed to (1) test methods which would provide reliable estimates of colony densities of different species of ants and (2) evaluate factors affecting spatial and temporal fluctuations in species densities of actively foraging ant species.

SITE DESCRIPTION. The data for this study were collected during the eleven month period of January 1973 through November 1973, on the Jornada Validation Site. The Jornada Validation Site is a watershed draining two slopes of a mountain in the Doña Ana Range located on the New Mexico State University Ranch, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. Two sites were selected for study at the validation site: the playa fringe (ca. 36 ha) and the bajada (ca. 25 ha).

On the playa fringe, mesquite (*Prosopis glandulosa*) and soap tree yucca (*Yucca elata*) are the dominant species on the basis of biomass, with densities of approx-

imately 480 individuals per hectare and 150 individuals per hectare respectively. Subdominant shrub species include snakeweed (*Xanthocephalum sarothrae*) and long leaf mormon tea (*Ephedra trifurca*). All species show spatial differences in distribution: mesquite exhibits its greatest cover on the north fringe of the playa and mormon tea on the south and east fringes.

Most of the soil on the playa fringe are sandy with a caliche (calcium carbonate deposition) layer about 100 cm from the surface (Soils I, III, IV and V, Fig. 1). On the west side of the playa (Soil VI) sandy soil has an over-layer of dark silt clay (Fig. 1).

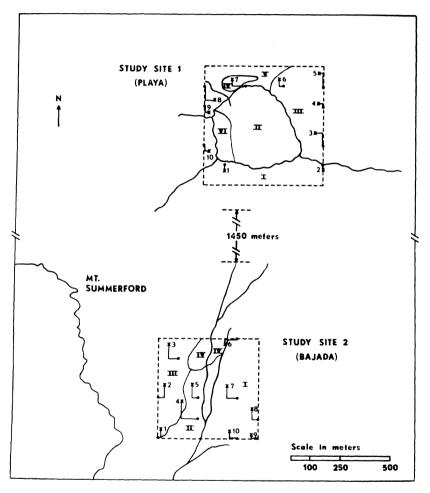


Fig. 1. Map of the Jornada Validation Site showing locations of ant census stakes and soil types. Playa soils I, III, IV and V are variously colored sands, soil II is a silt-clay and soil III is a sand with an overlayer of dark-silt. Bajada soils II and III are shallow sands with caliche less than 100 cm from the surface. Bajada soils I and IV are deeper sands.

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On the bajada, creosotebush (*Larrea divaricata*) is found at a density of 4,800 individuals per hectare, and mesquite (*Prosopis glandulosa*) at a density of 27 individuals per hectare. Of the grasses bush-muhley (*Muhlenbergia porteri*) is found at the greatest density, and of the succulents, soap tree yucca (*Yucca elata*) contributed the greatest biomass.

The bajada soils vary greatly. The soils on the east of the arroyo (Soil I, Fig. 1) are deeper sand with caliche at depths of over 100 cm. Soils on the west side of the arroyo are light colored shallow sands with caliche layer varying from 30 cm to 100 cm (soils II and III, Fig. 1). Soil IV (Fig. 1) is a sand alluvium with caliche at greater than 100 cm.

METHODS. Ten stakes were randomly located on each site. Using the stake as a center point, each area was divided into four quadrants.

In each quadrant a square meter frame was placed on the ground and the colonies of smaller ant species were recorded. These quadrant samples were located four meters from the stake. This provided a total sample area of 40 m^2 for each site.

For population estimates of the larger species, the quarter method was used (Cottam and Curtis 1956). The nest nearest the stake in each quadrant was located and the distance to the stake recorded. An average distance than then computed. This distance squared yielded the area containing one nest. This was then converted to number of nests per hectare.

Field identifications of ant species were made whenever possible. Otherwise, individual workers were brought into the laboratory and identified. No distinction was made in the survey data between *Myrmecocystus depilis* and *Myrmecocystus mimicus*, as distinguishing these two species always requires microscopic examination and was not considered feasible for a field study such as this. *Pheidole* colonies could not be identified to species, as it was often not possible to obtain both major and minor workers from a colony. *Pheidole* species recorded as being present at the Jornada Validation Site include *desertorum*, *militicida*, *rugulosa* and *xerophila* (Kay, pers. comm.).

Because of the sparseness of ant colonies, only the quadrat method was employed on the bajada. Estimates of numbers of colonies of large ant species on the bajada were from direct counts. Both types of census techniques were employed on the playa fringe.

RESULTS AND DISCUSSION. The major differences in species composition in the ant faunas of the two areas studied involved the larger harvester ants of the genus *Pogonomyrmex* and *Formica* (Fig. 2). Although colony densities were greater on the playa fringe than on the bajada, the small body size species (*Conomyrma, Iridomyrmex* and *Pheidole*) were represented on both sites (Fig. 3).

The small omnivorous ant species, *Iridomyrmex pruinosum*, *Conomyrma bicolor* and *Conomyrma insana* achieved high densities on both the playa and bajada. These three species combined reached estimated peak densities of 2,800 colonies per hectare on the playa and 1,100 colonies per hectare on the bajada. Peak densities of seed forag-

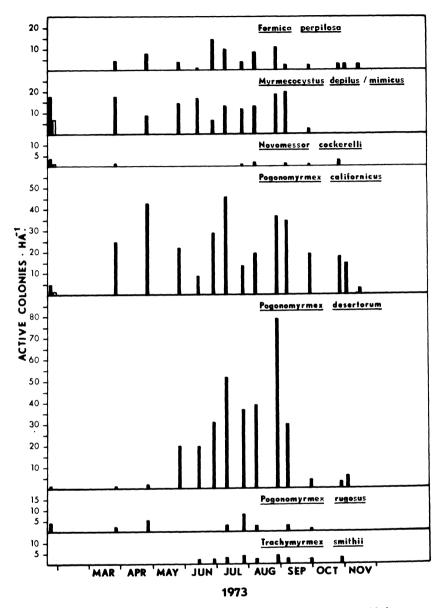


Fig. 2. Seasonal variation in densities of active colonies of ant species with large conspicuous and large body size foragers. Densities were estimated by the point-quarter method (Cottam and Curtis, 1956).

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ing species (*Pogonomyrmex* and *Pheidole*) were much lower on both the playa and bajada reaching estimated peak densities of 340 colonies per hectare on the playa and 520 colonies per hectare on the bajada. However, *Pheidole* species accounted for nearly the entire seed harvesting fauna on the bajada (Figs. 2 and 3).

Rainfall events seemed to effect individual species on the playa to a greater extent than those on the bajada. The largest numbers of total colonies recorded on the playa were observed during two censuses taken immediately after rainfall events on 9 July and 8 August. Species exhibiting greatest response to such events were the harvesters,

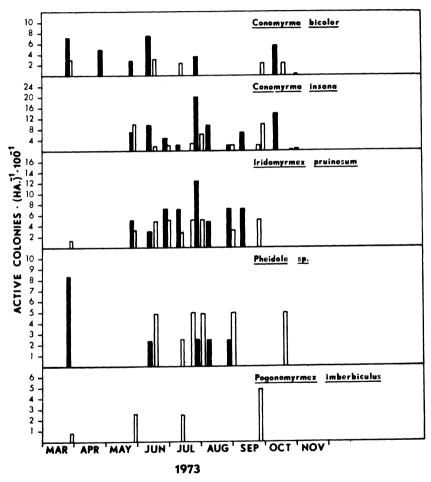


Fig. 3. Seasonal variation in densities of active colonies of ant species with small nests and small body size. Densities were estimated by square meter quadrats.

Pogonomyrmex californicus and Pogonomyrmex desertorum. Also responding with a meaningful increase in density were the small species of *C. insana* and *I. pruinosum*.

The largest numbers of total colonies on the bajada were recorded one day after rainfall events; 13 June and 1 August. Rainfall events at this site appeared to result in a more general increase in active colonies of small species instead of dramatically influencing populations in one or two species as on the playa. This difference could be accounted for by the difference in soil types between the two sites. The bajada represents an area of water run off and the playa an area of water run on. In addition the finer sands of the playa fringe have greater water retention than do the bajada soils. Therefore, the effect of a rainfall event on soil moisture on the bajada was not as long lasting as the effect on the playa.

Patterns of distribution varied with individual species. *Formica perpilosa* was found at the base of mesquite shrubs in areas where soils were loamy with an overwash layer of dark silt.

Pogonomyrmex imbericulus nests were invariably found at the bases of shrubs on the edges of small arroyos. Trachymyrmex smithi neomexicanus nests were found at the base of shrubs on the playa, often in the same areas inhabited by F. perpilosa. On the bajada, the nests of T. s. neomexicanus were usually located on arroyo banks.

The harvesters *P. californicus* and *P. desertorum* inhabited deeper sandy soils which support annual vegetation. These harvester ants prefer seeds of annual buckwheats which are limited to these deeper soils.

Iridomyrmex pruinosum and C. insana were found to be generally distributed over the entire area of both sites. Neither of these species exhibits specialized food preferences. I. pruinosum forages on plant exudates, attacks lone foragers of other species, and exhibits extensive scavenger behavior. C. insana also forages on plant exudates and other insects.

The presence of colonies of *Crematogaster* sp., *Pogonomyrmex* apache and *Solenopsis xyloni* were recorded, but numbers were not appreciable enough to yield any conclusive data.

Species never located in quadrant samples but recorded as present at the Jornada Validation Site include Componotus sp., Leptothorax sp., Myrmecocystus mexicanus, Myrmecocystus navajo, Neivamyrmex nigrescens, Solenopsis aurea and Solenopsis drockowi (Kay, pers. comm.). The absence of some species in survey data can be explained by their activity times. For example, M. navajo and M. mexicanus are both nocturnal species. Other species probably did not appear on the surveys due to their rarity and the concealment of colony sites.

The ant fauna could be divided into groups on the basis of seasonal activity patterns. Species that were principally midsummer active species included *P. desertorum, C. insana, M. depilus, M. mimicus* and *I. pruinosum* (Figs. 2 and 3). Other species were active over the year when air temperatures exceeded 20 C and soil temperatures at 20 cm ranged between 5 and 10 C. Species active earliest in the year included Novomessor cockerelli, *P. rugosus, P. californicus, P. imberbiculus,* and *F. perpilosa* which exhibited periodic activity from mid-February when environmental conditions were favorable.

Significantly fewer colonies of *C. bicolor* were active during July and August when *C. insana* had the greatest number of active colonies.

A similar pattern was observed in *P. californicus* and *P. desertorum*. Although *Pogonomyrmex* species exhibited no physiological difference in tolerance range (Whitford, unpubl. data), these species exhibited differences in both seasonal and daily foraging activity patterns. *P. californicus* foraging in midsummer is largely limited to periods of highest temperature around midday when *P. desertorum* foraging is reduced or has ceased. In spring and fall, *P. californicus* was active over the entire day.

These observations provide indirect evidence of competition between P. californicus, and P. desertorum and between C. insana and C. bicolor. These species have similar habitat requirements, almost completely overlap in food requirements (Whitford, unpubl. data), but coexist by dividing these resources by temporal separation of peak foraging on a seasonal basis.

These densities of active ant colonies suggest that the ant community may have an important function in energy flow and nutrient turnover in desert ecosystems. Many species are omnivorous (Conomyrma, Myrmecocystus and Iridomyrmex) and thus may be important as predators of other arthropods as has been demonstrated in a meadow ecosystem (Kajak, et al. 1971). We have estimated forager numbers of over 1,000 per colony in Pogonomyrmex, Novomessor and F. perpilosa (Whitford, Ettershank, Schumacher, Unpubl. Data), and based on our observations of foraging in Conomyrma, Myrmecocystus, and Iridomyrmex, we would estimate similar forager numbers as minimum values for these species. Seed harvesting ants have been shown to account for the removal of a significant fraction of the seeds produced in a given year (Ludwig and Whitford 1974). Ants represent the most numerous insects in Chihuahuan desert ecosystems with the possible exception of termites. They are important as seed consumers, predators and scavengers; thus, operating at several trophic levels in the system.

Although we did not intensively study the nocturnal ant fauna, we did collect some data on nocturnal species. One species, $Myrmecocy-stus\ mexicanus$, occurs at densities of one colony per hectare on both the playa and bajada. These estimates were obtained by direct counts of the very distinctive nest cones of this species. This species is strictly nocturnal and active much of the year whenever soil surface temperatures are above freezing (C. A. Kay, pers. comm.). N. cockerelli and T. s. neomexicanus are primarily nocturnal foragers in midsummer as do some species of Pheidole. Another strictly nocturnal species which is rare on the sites in M. navajo. Therefore, the data in this paper represents an accurate picture of seasonal variation in densities of active ant colonies in spite of a lack of intense effort to make density estimates at night.

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