Insectes Sociaux, Paris.
1978. Tome 25, n° 1, pp. 79-88.

STRUCTURE AND SEASONAL ACTIVITY OF CHIHUAHUA DESERT ANT COMMUNITIES

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Reçu le 22 novembre 1976. Accepté le 12 janvier 1977.

SUMMARY

In a desert area with abundant annual plants the largest feeding guild was gramnivores (nine species). In an area with few annual plants, the largest feeding guild was omnivores (eight species). Within a guild there is little overlap in body length of workers. Species in which there was overlap in body length of workers exhibited marked differences in diel and seasonal activity. Variation in precipitation and productivity between years resulted in differences in seasonal activity, hence considerable variation in the structure of the ant community through time.

RÉSUMÉ

La structure et l'activité saisonnière des sociétés de fourmis de la région désertique de Chihuahua.

Dans une région désertique où les plantes annuelles sont abondantes, les sociétés de Fourmis granivores sont les plus nombreuses (neuf espèces). Dans une région où les plantes annuelles sont rares, les sociétés les plus fréquentes sont omnivores (huit espèces). Au sein d'une même société, il y a peu de différences dans la taille des ouvrières. Les espèces où la taille des ouvrières varie beaucoup, présentent des différences importantes dans leur activité journalière et saisonnière. Des variations de pluviosité et de productivité d'une année à l'autre engendrent des variations d'activité saisonnière, et, par conséquent, des différences importantes dans la structure de la société de Fourmis tout au long de l'année.

INTRODUCTION

Studies of entire ant faunas have been largely concerned with species packing (CULVER, 1974; LEVINS *et al.*, 1973) or with patterns of dispersion (BARONI-URBANI, 1969; BRIAN, 1964, 1956) thus based on data collected over short time periods. Most studies of surface activity in ants have concentrated on diel activity (TALBOT, 1946; MCCLUSKEY, 1972; DEBRUYN and DEBRUIN, 1972; ROGERS, 1974; LIEVIEUX, 1975; WHITFORD and ETTERSHANK, 1975) although seasonal patterns have been shown to differ in desert seed harvesting ants (BERNSTEIN, 1974; WHITFORD and ETTERSHANK, 1975). A study by MARKIN *et al.* (1974) reported that seasonal activity in the imported fire ant, *Solenopsis saevissima* was uniformly temperature dependent in all parts of the range. SANDERS (1972) concluded that seasonal shifts in daily activity in *Camponotus* spp. was temperature dependent. BENOIS (1973) reported seasonal differences in behavior and population dynamics of the Argentine ant, *Iridomyrmex humilis* in southern France.

The marked between year differences in seasonal availability of food resources and seasonal fluctuations in microclimate that approach the tolerance limits of species in desert ecosystems suggests considerable variation in seasonal activity patterns of many desert organisms. CREIGHTON (1950) stated that prolonged drought caused extensive aestivation of many ants in the canyons of the Chicos Mountains in Big Bend National Park, Texas. CREIGHTON's suggestion that numbers of active colonies of ants might be related to rainfall was supported by the data of WHITFORD and ETTERSHANK (1975) for seed harvesting ants. Here I examine the trophic structure and the seasonal activity patterns of two ant communities in the northern Chihuahuan desert in relationship to rainfall and productivity patterns.

STUDY AREA

Studies were conducted on the Jornada Validation Site, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. The Jornada Validation Site is a desert watershed which drains into a small dry lake. The watershed varies in elevation from ca. 2,000 to 1,000 m. The 100 year annual rainfall average $\pm$ one standard deviation at the New Mexico State University Station, Las Cruces, New Mexico, is 211 ± 77 mm (HOUGHTON, 1972), with most of that rainfall occurring during late summer from convectional storms. Summer maximum temperatures reach 40 °C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

Numbers of active colonies of ants were censused on two sites approximately 1.5 km apart. One site (designated playa) of approximately 36 ha included the area around the dry lake and the other was located on the alluvial fan of the upper watershed (designated bajada). The vegetation of the playa is predominately mesquite *(Prosopis glandulosa)* at a density of 480 ha^{-1} and soaptree yucca *(Yucca elata)* at a density of 150 ha^{-1}. Subdominant shrubs include long leaf mormon tea *(Ephedra trifurca)* and snakeweed *(Guttierrezia sarothrae* and *Guttierrezia microcephala)*. Soils are sandy with calcium carbonate deposition layers at ca 100 cm below the surface.

The 25 ha bajada is predominantly low shrubs, creosotebush *(Larrea tridentata)* at a density of 4,800 ha^{-1}. The bajada is dissected by numerous dry water courses which are bordered by tarbush *(Flourensia cernua)*, banana yucca *(Yucca baccata)*, mesquite and soaptree yucca. The bajada soils are sandy alluvium of varying depth (30 cm to 100 cm) over calcium carbonate deposition layers.

METHODS

A variety of sampling methods were used to obtain density estimates of active ant colonies, i.e. nests with open entrances through which workers were observed entering and leaving). Most species were sampled by recording the numbers of active colonies by species within a square meter frame placed at random points on the surface. Points were selected at random but stratified to include at least two points per hectare. Low density, large conspicuous nest species were sampled by the point quarter method (Cottam and Curtis, 1956) in which distances from random points to nests in each quadrat were recorded and averaged to compute relative density. A minimum of 20 points were done on each site.

Night sampling was done along fixed belt transects selected to provide adequate representation of variation in topography and vegetation on each site. Belts were of variable length and 2 m wide. A total of at least 4,000 m^2 of transect were sampled on each site. No night transects as defined above were run during 1973 but observations were made on patterns of nocturnal activity.

Field identification of species was made whenever feasible. Species which were not readily identifiable in the field were collected in vials and taken into the lab for identification. No distinction was made between the two congeneric species, *Myrmecocystus depilis* and *Myrmecocystus mimicus*, since there are few discernible differences. Likewise, species names for the genus *Pheidole* were omitted as the major and minor workers necessary for identification were often not collectible.

RESULTS

Species encountered in this study were assigned to a feeding guild based on our observations and descriptions of general biology from the literature (table I). In Chihuahuan desert ecosystems gramnivorous species are as numerous as omnivores. Two species assigned to the omnivore guild, *Novomessor cockerelli* and *Solenopsis xyloni*, forage on seeds approximately 25 % of the time. Within guilds, workers separate on the basis of length with few exceptions, i.g., *Conomyrma bicolor* and *Conomyrma insana*, *Pogonomyrmex desertorum* and *Pogonomyrmex californicus*. Strictly diurnal species are limited to four *Pogonomyrmex* sp. and only three species are strictly nocturnal (table I).

The differences in seasonal activity in the species studied are best understood in relationship to rainfall, availability of seeds of annual plants and relative abundance of insects (table II) (fig. 1 and 2). Dry conditions in early summer

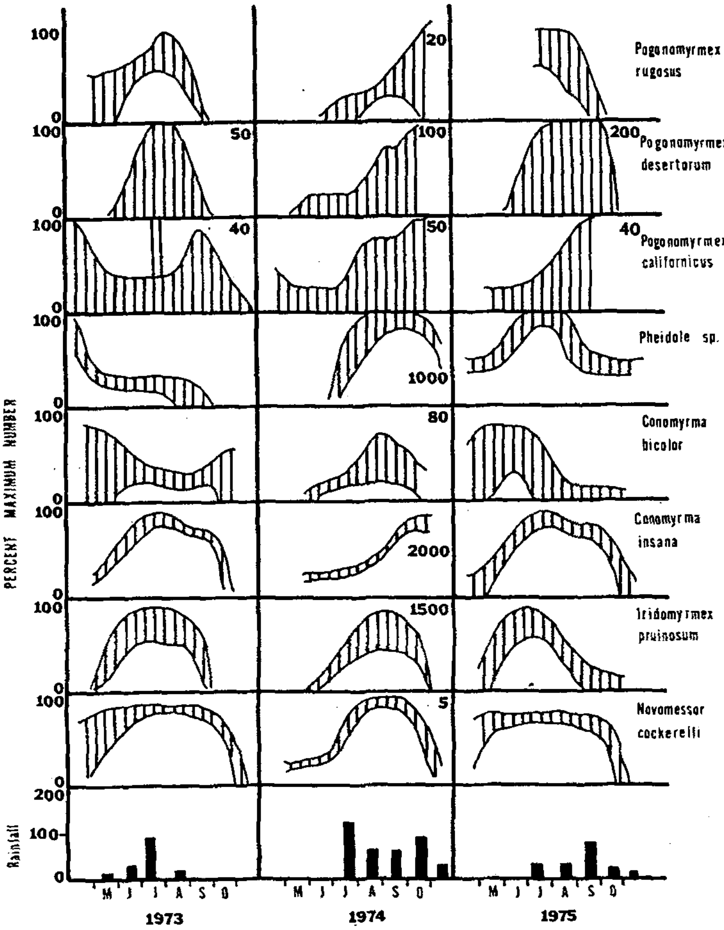

FIG. 1. — The variation in relative abundance of active colonies of ant species in the three years of the study expressed as a percent of the maximum density with monthly rainfall presented for reference. The number associated with each species in the body of the graph expresses the maximum density in numbers per hectare, where maximum density varied significantly between years, numbers are recorded for each year. Numbers of colonies active at night are shown by the unlined area and numbers of colonies active in the day are shown by the lined area plus the unlined area. For example, *Pogonomyrmex rugosus* is both diurnal and nocturnal, *Pogonomyrmex desertorum* is only diurnal while *Myrmecocystus mexicanus* is strictly nocturnal.

FIG. 1. — Les variations dans l'abondance relative du nombre de colonies actives appartenant à plusieurs espèces de Fourmis, durant les trois années de notre étude, sont exprimées en pourcentage de la densité maximale en fonction de la pluviométrie. Les chiffres qui figurent dans les graphiques correspondent à la densité maximale du nombre de colonies par hectare. Lorsque la densité maximale varie d'une année à l'autre de façon significative; le nombre de colonies est indiqué pour chaque année. Les sociétés actives pendant la nuit sont indiquées par les zones blanches, alors que les sociétés actives dans la journée sont figurées par les zones hachurées plus les zones blanches. Par exemple, *Pogonomyrmex rugosus* est à la fois nocturne et diurne; *Pogonomyrmex desertorum* est seulement diurne, alors que *Myrmecocystus mexicanus* est seulement nocturne.

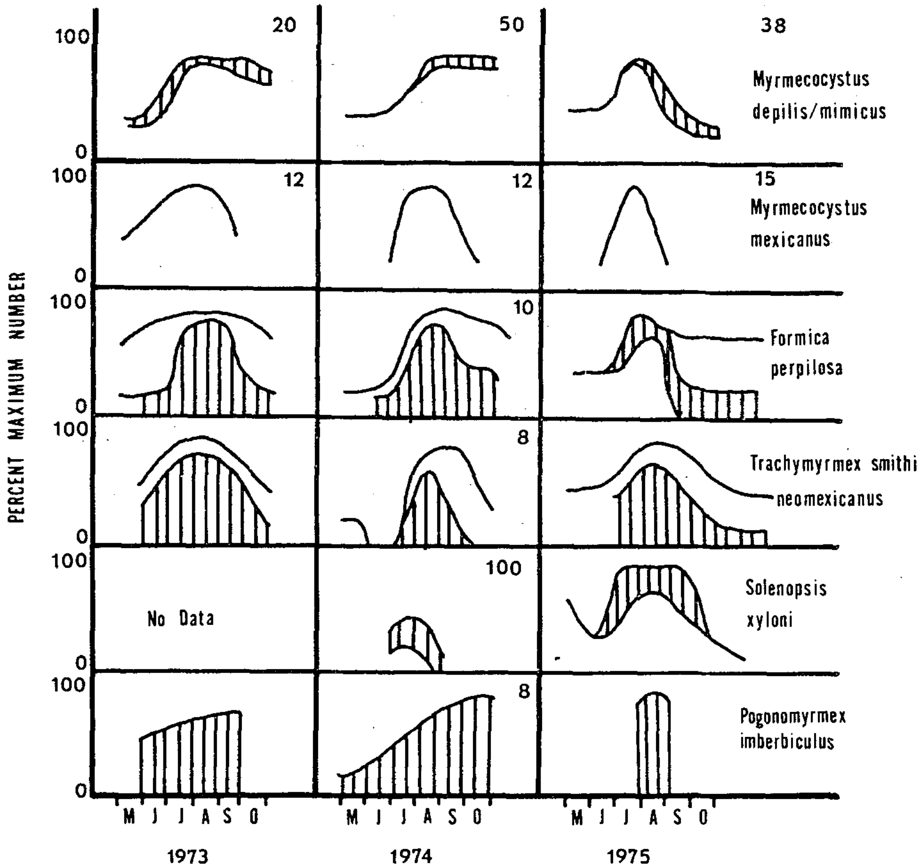

FIG. 2. — The relative abundance of active colonies of ants expressed as a percent of the maximum density. Method of presentation the same as figure 1.

FIG. 2. — L'abondance de sociétés actives de Fourmis est exprimée en pourcentage de la densité maximale. La représentation est la même que dans la figure 1.

(May and June) and absence of spring and early summer annual plants and insects in 1974 resulted in shifts from the typical pattern in a number of species. This change was most pronounced in species like *P. desertorum* and *C. insana* which normally reach peak activity in mid-summer (fig. 1 and 2).

In species which were both nocturnal and diurnal, there was considerable fluctuation in relative numbers of active colonies. Occasionally there were more colonies active at night than during the day. However, the patterns presented in figures 1 and 2 ignore these occasional departures from the typical behavior. For example, in mid-summer approximately half of the *P. rugosus* colonies were active at night. On several dates in 1976, we recorded *P. rugosus* active at night when none were active during the day.

TABLE I. — Relative abundance of ant species assigned to four feeding guilds in two northern Chihuahuan desert communities. Relative abundance is indicated as follows : *** common, occurring at high densities or in large colonies; ** occurring at moderate densities; * present at low densities. D indicates those species which are strictly diurnal and N those which are strictly nocturnal.

TABLEAU I. — Abondance relative des espèces de fourmis qui vivent dans deux ensembles de populations du désert de Chihuahuan. Les espèces sont classées en cinq groupes, selon leur régime alimentaire. L'abondance est ainsi représentée : *** la densité est élevée ou les sociétés sont de grande taille; ** la densité est moyenne; * la densité est faible. D indique les espèces diurnes et N les espèces nocturnes.

Feeding guild	Worker length range in mm	Creosotebush bajada	Mesquite-yucca grassland playa
Gramnivores (seed feeders) :			
Pogonomyrmex rugosus	6.5-9.5	*	***
Pogonomyrmex desertorum	5.0-7.5	D*	***
Pogonomyrmex californicus	4.5-6.5	D*	**
Pogonomyrmex apache	7.5-8.5	D	*
Pogonomyrmex imberbiculus	3.8-4.0	D*	**
Pheidole desertorum	2.9-3.8	*	*
Pheidole militicida	2.5-4.0	*	**
Pheidole rugulosa	1.5-1.7	**	***
Pheidole xerophila	1.8-2.4	**	***
Honeydew-exudate feeders :			
Myrmecocystus mimicus-depilis	3.0-5.5	**	***
Myrmecocystus mexicanus	4.0-8.5	N**	**
Myrmecocystus navajo	3.0-4.5	N	*
Omnivores :			
Novomessor cockerelli	8.5-9.8	**	***
Formica perpilosa	5.0-8.5		**
Conomyrma bicolor	2.8-4.0	**	***
Conomyrma insana	2.5-3.8	**	***
Iridomyrmex pruinosum	1.8-2.5	**	***
Solenopsis xyloni	2.5-3.1	*	**
Solenopsis aurea		*	*
Solenopsis krockowi	<2.5	*	*
Crematogaster sp.		*	
Detritivores :			
Trachymyrmex smithi neomexicanus	8.5-9.8	**	**
Predators :			
Neivamyrmex nigrescens	3.5-5.0	N*	

TABLE II. — Quarterly rainfall in mm, relative abundance of mature annual plants (+ present; ++ abundant) and relative abundance of insects (* present; ** abundant).

TABLEAU II. — Pluviométrie trimestrielle exprimée en mm. L'abondance des plantes annuelles parvenues à maturité est ainsi représentée : + présentes; ++ abondantes. L'abondance des insectes est représenté par : * présents; ** abondants.

	1973	1974	1975
January-March	66.0	22.4	33.5 +
April-June	44.7 +*	0.5	2.8 +
July-September	11.0 ++**	229.8 +**	136.7 +**
October-December	2.8 +*	92.2 +*	27.9 +*

Species exhibiting both diurnal and nocturnal activity also had different diel patterns. Most species were bimodal with peaks in the early daylight hours and 2-3 h after sunset. Nearly all ceased activity at mid-day in the summer when soil surface temperatures exceeded 50 °C for 2-4 h. *Trachymyrmex smithi neomexicanus* and *Pheidole militicida* exhibited a single peak just before dawn. Most of these species which exhibited both diurnal and nocturnal activity were strictly or predominately diurnal in spring and fall (fig. 1 and 2). Two species were predominately nocturnal: *Formica perpilosa* and *T. s. neomexicanus.* Detailed analysis of variation in diel activity of many of these species is presented in SCHUMACHER and WHITFORD (1976).

Diurnal species exhibited greater differences in seasonal activity between years than did most other species.

DISCUSSION

The largest feeding guild in the mesquite-yucca community was the gramnivore guild. The most important guild in the creosotebush community was the omnivores. The bajada is an area of shallow soils and water run-off which supports few species of annual plants at low densities (nine species, 3,156 ha^{-1} in September, 1974: WHITFORD, 1975). The playa has deeper soils and is an area of water accumulation which supports a larger number of species and high densities of annuals (20 species, 116,000 ha^{-1} in September, 1974: WHITFORD, 1975). This diversity and density of annuals produces quantities of seeds of various sizes which can be exploited by the gramnivorous guild. The seasonal abundance of annuals and species composition of annuals varies depending upon rainfall amount and distribution. Between year differences in seasonal activity in the gramnivores is related to the availability of seeds (WHITFORD and ETTERSHANK, 1975). The relative importance of omnivores when compared to gramnivores on the bajada reflects the relative proportion of insects, plant exudates, and seeds of annuals in the two areas. The lower relative abundance of all species on the bajada reflects the lower productivity of that area in comparison to the playa (WHITFORD, 1975). The species occurring at the same relative abundance on both sites were a detritivore, *T. s. neomexicanus* and a predator, *Neivamyrmex nigrescens.*

The *Pogonomyrmex* and *Pheidole* species can be separated by worker size with little size overlap except in *Pogonomyrmex desertorum* and *P. californicus* and *Pogonomyrmex apache* and *P. rugosus.* WHITFORD and ETTERSHANK (1975) and data from this study suggest that competition between *P. desertorum* and *P. californicus* is avoided by differences in diel and seasonal forage times. *P. apache* colonies occur at low densities in areas where *P. rugosus* is absent (flood zones at the edge of the dry lake). DAVIDSON (in press) has shown seeds selected by workers of *Pheidole* and *Pogonomyrmex* are related to body size of the workers. Thus, competition in the gramnivore guild appears to be reduced primarily by differences in body size and secondarily by temporal differences in foraging behavior.

As with gramnivores, there was only slight overlap in worker sizes among omnivores except in *C. insana* and *C. bicolor* which had different seasonal foraging peaks. This suggests that omnivores may be dividing resources on size, as has been shown for the gramnivores.

In the pairs *C. bicolor/C. insana* and *P. desertorum/P. californicus,* the species in each pair reaching the highest density are the species most active in mid-summer. Although the congeners are capable of activity during mid-summer, the reduced numbers of active colonies is probably due to competition. The species in each pair relegated to spring and fall activity generally have lower resources in spring and fewer foraging hours in fall due to temperature constraints. These factors combine to reduce the numbers of colonies of these species which the area can support.

The large number of species exhibiting both nocturnal and diurnal activity and variation in degree of nocturnality suggests that such flexibility is important to many desert ant species. The strictly diurnal species are seed feeders and strictly nocturnal are predators or largely predatory *(Myrmecocystus* spp.*)*. Species like *P. rugosus* and *N. cockerelli* forage primarily on insects at night but take seeds during the day (WHITFORD and ETTERSHANK, 1975 and unpublished data). SANDERS (1972) suggested that the shift to crepuscular and/or nocturnality in *Camponotus* spp. was a temperature adaptation in these ants in northwestern Ontario. While avoidance of high temperatures and saturation deficits in the desert is an advantage accrued to nocturnal species, the increased availability of insects as prey must also be considered. Nocturnal foraging in *P. rugosus* and *N. cockerelli* provides insect protein which may be essential to production of large broods in these species which are characterized by large numbers of foragers per colony (WHITFORD and ETTERSHANK, 1975).

Nocturnal foraging in *F. perpilosa* may also be related to the greater activity, hence availability of insects at night. Thus, nocturnal foraging may provide insect protein to some species while in others it may be a behavior which allows avoidance of thermal stress and dehydration.

Unlike the study reported by MARKIN *et al.* (1974) and SANDERS (1972) seasonal activity in desert ants is not temperature dependent. In desert species temperature acts as a threshold for seasonal foraging activity but not as a regulator. Some species are more affected by rainfall than others. For example, the species of *Pheidole, Ph. desertorum, Ph. rugulosa* and *Ph. militicida* exhibit peak activity within a few hours after rainfall. However, unless abundant forage is available, these species do not remain active. Reduction or absence of surface activity during periods of scarce resources and/or high saturation deficit is an adaptive behavioral response in an unpredictable environment like a desert.

This study demonstrates that the structure (relative abundance, etc.) of desert ant communities cannot be accurately assessed at one point in time nor can between year comparisons be made by estimates made on the same date in different years. The surface activity of desert ants is controlled by a variety of factors : temperature, light (time of day), humidity, forage availability and competition (WHITFORD and ETTERSHANK, 1975; SCHUMACHER and WHITFORD, 1974, 1976). The interactions of these factors result in variation in seasonal activity between years and hence the structure of desert ant communities. Species packing in this desert ant fauna is accomplished primarily by body size differences in foragers but seasonal differences in activity also contributes. The trophic structure of the ant community varies seasonally reflecting the availability of types of food and the nutritional requirements of the species.

ACKNOWLEDGEMENTS. — This study was supported by the US/IBP Desert Biome Program under Grant GB 15886 from the National Science Foundation. Martha BRYANT, Dirk DEPREE, Elaine DEPREE, Patrick HAMILTON, Priscilla JOHNSON and Richard JOHNSON assisted with the field work.

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