TEMPORAL FLUCTUATIONS IN DENSITY AND DIVERSITY OF DESERT RODENT POPULATIONS

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ABSTRACT.—Species composition and density were studied in two areas on a watershed in the Chihuahuan Desert in southern New Mexico. The upper portion of the watershed, a creosotebush community, supported "resident" populations of *Dipodomys merriami, Perognathus penicillatus, Neotoma* sp., and *Onychomys torridus.* The lower portion of the watershed, which drained into a grass-covered dry lake, supported *Sigmodon hispidus, Reithrodontomys megalotis, Dipodomys ordii,* and *Spermophilus spilosoma,* in addition to the species found in the creosotebush area.

Most "resident" species responded to fluctuations in rainfall and primary production by reduction in density during drought periods and a 10 to 12 month lag in population recovery during extended periods of favorable rainfall and plant production. Transient species such as *Peromyscus* sp. and *Mus musculus* established breeding populations on both sites during periods of more mesic conditions and reached densities that exceeded those of "resident" species. The rapid increase in population numbers of transient species when compared to the resident heteromyids was due to the higher reproductive potential of the cricetids. The species diversity index (H') nearly doubled during a period of above average rainfall which was proceeded by drought. Changes in species diversity in time was correlated with rainfall and productivity. The dynamics of these Chihuahuan Desert rodent communities are considered in terms of immigration and extinction as the suitability of habitat islands change through time.

Numerous studies have dealt with short-term dynamics of rodent populations, and factors involved in regulation of population density and have recently been reviewed in Grant (1972), Mazurkiewicz (1972), M'Closkey (1972), and MacMillen (1964). Studies of entire rodent communities over a number of years are limited to a relatively few studies (Chew and Chew, 1970; French *et al.,* 1974; Gentry *et al.,* 1971). The Desert Biome, US/IBP, program provided an opportunity to study rodent populations over several years in two Chihuahuan Desert ecosystems which are part of a single watershed. This allowed evaluation of changes in species diversity and density as affected by climate, plant production and phenology, and fluctuations in population densities of other animals.

Because of the stochastic nature of this desert climate, marked fluctuations in density were expected, but rapid shifts in the species composition component of diversity were not expected (Rosenzweig and Winakur, 1969). Long-term population studies allow evaluation of processes that promote stability in what ostensibly appears to be an unstable system. These studies also provided examples of competitive interactions, and material to examine the processes of immigration and extinction on habitat islands as a function of environmental change.
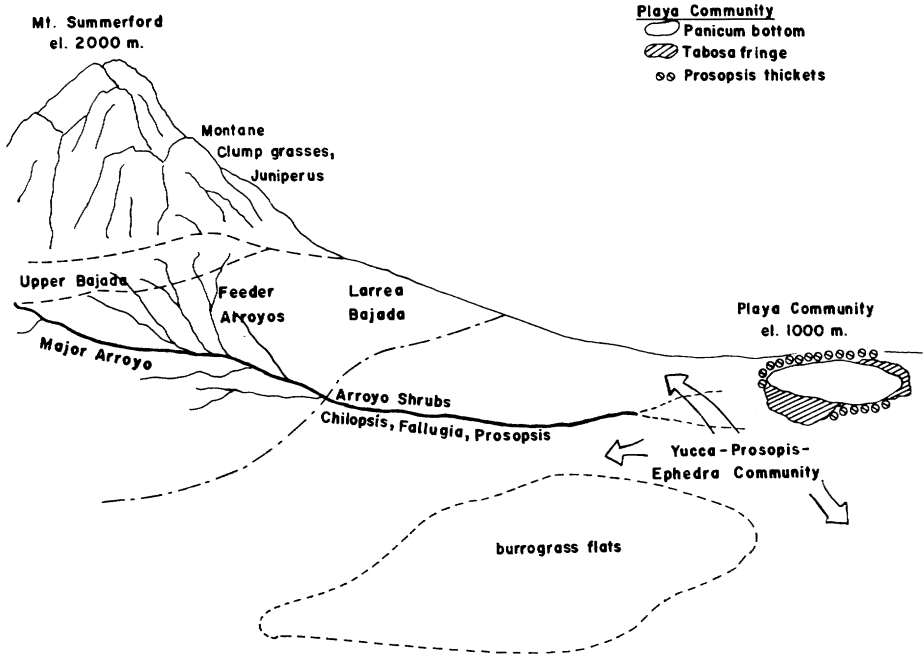
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FIG. 1.—Distribution of plant communities and topographic relationships of the Jornada Site Watershed in the Chihuahuan Desert.

METHODS

Rodent live-trapping studies were conducted on two sites on a desert watershed which drains into a small playa lake (Figs. 1 and 2). The watershed (Jornada Validation Site, Desert Biome, US/IBP) is located approximately 40 kilometers (km) NNE of Las Cruces, Doña Ana County, New Mexico.

The bajada site is located on gravelly alluvium from Mt. Summerford with soil depths over the caliche (calcium carbonate deposition layer) varying from a few centimeters to about 1 meter (m) in depth. The dominant shrub, creosotebush (*Larrea tridentata*), occurs on all of the drained slopes. The site is bisected by a large arroyo (water course) and numerous tributary arroyos which have dense fringing vegetation—mesquite, *Prosopis glandulosa*; soaptree yucca, *Yucca elata*; tarbush, *Flourensia cernua*; spanish bayonet, *Yucca baccata*; apache plume, *Fallugia paradoxa*; bush muhly bunch grass, *Muhlenbergia porteri*. The total perennial cover is 27.7 percent of which 84 percent is *Larrea*. Forbs and annual grasses are sparse and even under the most mesic conditions reach a maximum biomass of 2.1 kilograms (kg) per hectare (ha)$^{-1}$ or 2.3 percent of that produced on the playa below (Whitford, 1973).

The playa is a clay bottom depression of 19.6 ha with a cover of vine mesquite grass, *Panicum obtusum*. Drainage patterns produce two swales of tobosa grass (*Hilaria mutica*) at the edges of the playa (Fig. 1). The playa is surrounded by deep sandy soils with a caliche layer approximately 1 to 2 m below the surface. Dominant plants include dense thickets of mesquite, *Prosopis glandulosa*, at the playa edge (Fig. 1), and scattered *P. glandulosa*, mormon tea, *Ephedra trifurca*, and soaptree yucca, *Yucca elata*, on the fringe
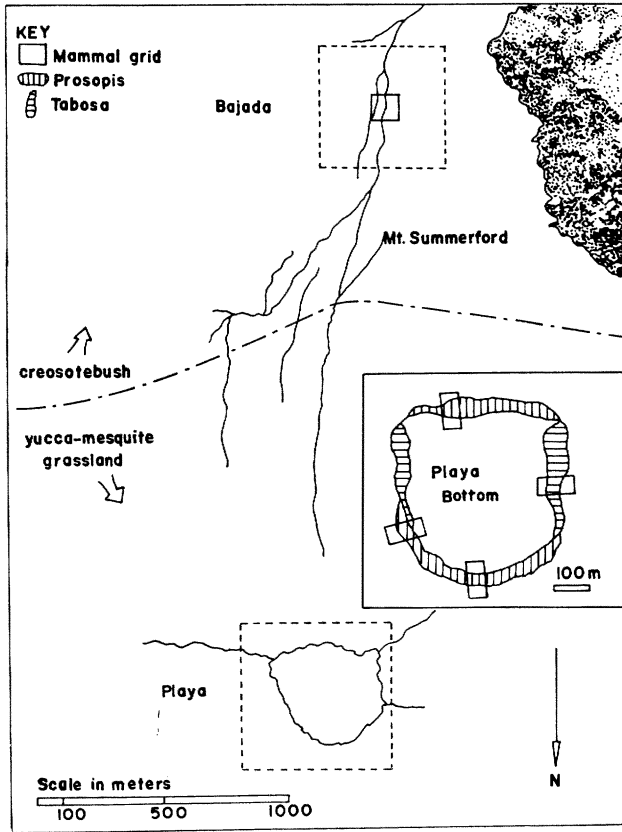
FIG. 2.—Location of trapping grids on the watershed with respect to plant communities and distances between study sites.

areas of the playa. The sandy soils support high densities of a variety of annual and perennial forbs and grasses when soil moisture is suitable.

The four trap grids on the playa were established with traps in five lines, 10 trap stations per line, with 15 m trap spacing (Fig. 2). The bajada grid was in 10 lines, 10 trap stations per line and 10 m trap spacing. Alternate stations were set with two traps per station; double trap stations were changed every trap night. Sherman live traps baited with cracked milo were used throughout the study.

Grids were trapped for four consecutive nights. Preliminary studies in 1971 showed that there was no significant increase in individual animals trapped between four and eight consecutive nights. Each individual was marked with a unique toe clip, sexed, breeding condition noted, weighed, and released. Densities were estimated using the mark-recapture data to calculate a Lincoln Index (Poole, 1974). The validity of various population estimators has been tested by simulation and discussed by Manly (1970, 1971). In simulation studies with varying population attributes, Ettershank and Ettershank (1973) demonstrated that the errors associated with individual Lincoln Index esimates were similar to those obtained by the Jolley stochastic model. Because of the nature of our trapping program
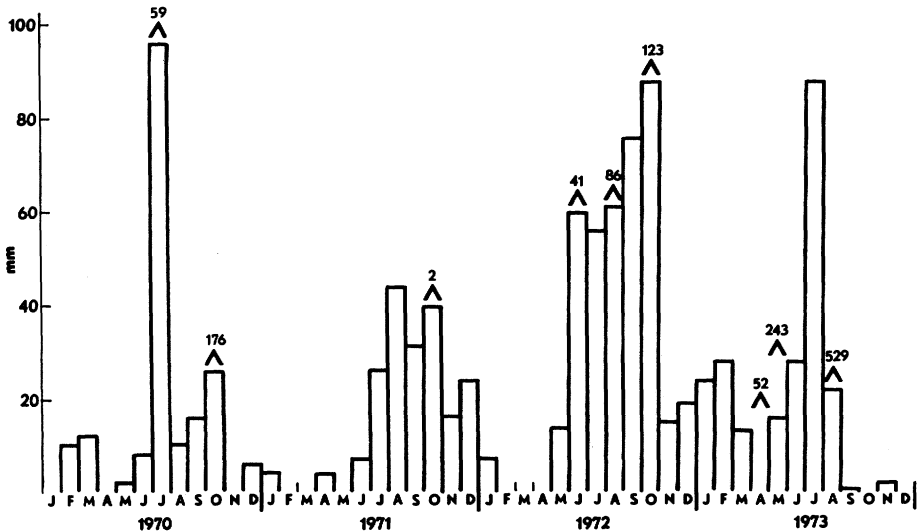
Fig. 3.—Monthly rainfall from 1970 to 1973 from the weather station at the playa site. The numbers above the bar graphs represent total standing crop biomass of grasses and forbs in kg per ha for the periods indicated.

we used individuals captured on days one and two as precensus and days three and four as census in applying the Lincoln Index.

Population densities for comparisons between playa and bajada were calculated using the area of suitable habitat for playa mammals to compute densities. Area sampled by grids in density estimates was the area of the grid plus half the diameter of a circular home range based on home range estimates from recapture radii.

RESULTS

The ultimate factor affecting the dynamics of rodent populations was rainfall pattern and its subsequent effects on vegetation and ultimately seed and insect production. The most important proximate factor appeared to be production of annual and perennial forbs and grasses. The relationships of rainfall to forb and grass production are summarized in Fig. 3. During the study, the area was subject to drought conditions from September 1970 through October 1971 and somewhat above average amounts of rainfall in 1972 and 1973 which were not restricted to the typical mid-summer rainy season (Houghton, 1972).

The results of our trapping program on the watershed suggested certain patterns of habitat utilization (Table 1). The relationships of "resident" species which maintained populations in an area under all observed environmental conditions to "immigrant" species which moved into habitat areas as their structures change according to changes in the climate are the key to understand the dynamics of these rodent populations.

TABLE 1.—*"Resident" species (R) which are capable of maintaining populations in three Chihuahuan Desert plant communities under minimal environmental conditions and immigrant species (I) which move into these communities under favorable environmental conditions. Absence is indicated by O.*

Species	Hilaria-Panicum	Prosopis-Ephedra-Yucca	Larrea
Dipodomys merriami	O	R	R
Dipodomys ordii	O	R	I
Dipodomys spectabilis	O	R	O
Perognathus penicillatus	O	R	R
Perognathus intermedius	O	I	R
Perognathus flavus	(R-I)	I	I
Peromyscus eremicus	O	I	R
Peromyscus maniculatus	(R-I)	I	I
Peromyscus leucopus	I	I	I
Mus musculus	I	I	O
Neotoma (albigula-micropus)	O	R	R
Reithrodontomys megalotis	R	I	I
Sigmodon hispidus	R	O	O
Onychomys torridus	O	I	R
Spermophilus spilosoma	O	R	O

Population changes in the three species of *Dipodomys* on the playa and bajada are summarized in Fig. 4. The data for 1970 are not as complete as those for the subsequent years because not all grids were established and trapped regularly until 1971. Densities of *Dipodomys merriami* were essentially the same on the playa and bajada and exhibited the same patterns of population change due to recruitment, immigration, emigration, and predation. Significant recruitment of young occurred only in late summer in both 1971 and 1972, but in 1973 recruitment occurred from March through October. The basic carrying capacity for *D. merriami* on both the playa and bajada appeared to be between 10 to 15 individuals per ha (Fig. 4). The survivorship of *D. merriami* recruited into the population during the drought year, 1971, was lower than those recruited during 1970, a year of close to average rainfall (Figs. 4 and 5).

Dipodomys spectabilis was a component of the playa fauna that only occurred at low densities on the playa fringe. This species disappeared from the trappable population from September 1971 until May 1973 (Fig. 4). In the autumn of 1971, we observed that their mounds had all been extensively excavated, apparently by badger, which probably accounted for their disappearance.

Dipodomys ordii exhibited a population increase in 1971 with high recruitment in summer of 1971. The drought and low productivity of 1971 apparently resulted in lowered survivorship of this species. It remained at low density (approximately one individual per ha) through 1972 then increased
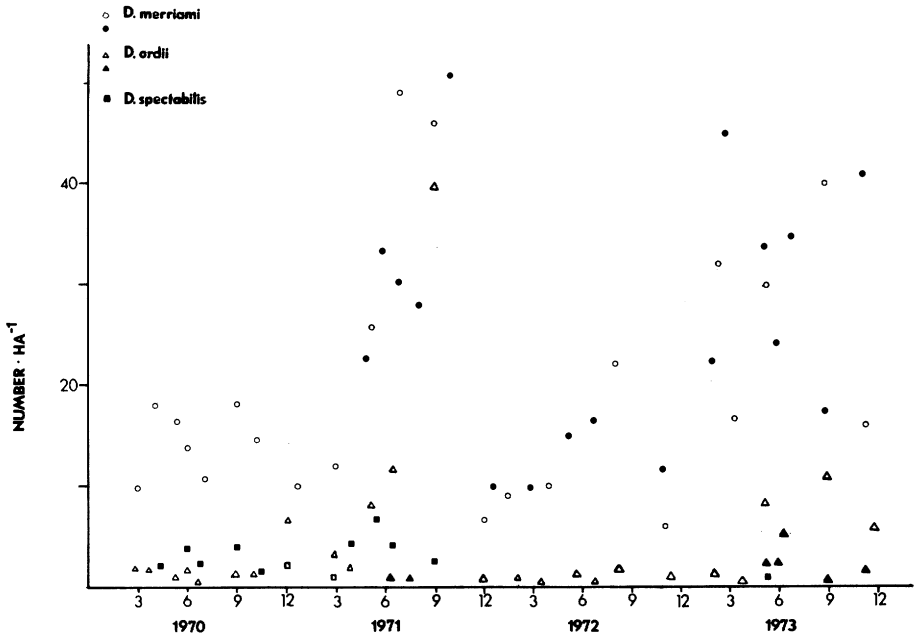
Fig. 4.—Population fluctuations in three species of *Dipodomys*. The open symbols represent density estimates of *Dipodomys ordii* and *Dipodomys merriami* on the bajada site. *Dipodomys spectabilis* was found only on the playa site.

to about five individuals per ha in 1973 following the second year of high productivity of forbs and grasses.

The occurrence of *D. ordii* on the bajada was limited to occasional immature migrants during periods of recruitment except in 1973 when several *D. ordii* established residence adjacent to the large arroyo and the same individuals remained in the trappable population for over 6 months.

Of other heteromyids in the Chihuahuan Desert rodent community, *Perognathus* exhibited population responses different from the *Dipodomys* (Fig. 6). Of the three *Perognathus*, *Perognathus flavus* exhibited the most erratic pattern of population change. *Perognathus flavus* was an established resident of playa bottom and immediate fringe appearing in the bajada samples only as a transient. *Perognathus flavus* exhibited a population explosion on the playa in 1971. When grids were checked at night, *P. flavus* were observed all over the playa bottom and were sufficiently numerous to capture by hand in the summer and early autumn, 1971. Following the recruitment peak in May 1971, *P. flavus* was taken on the bajada as a transient probably representing immigration from the playa. During the remainder of the study, *P. flavus* had low population densities (approximately 1 to 2 animals per ha) despite apparent favorable conditions of food availability and climate in 1972 and 1973.
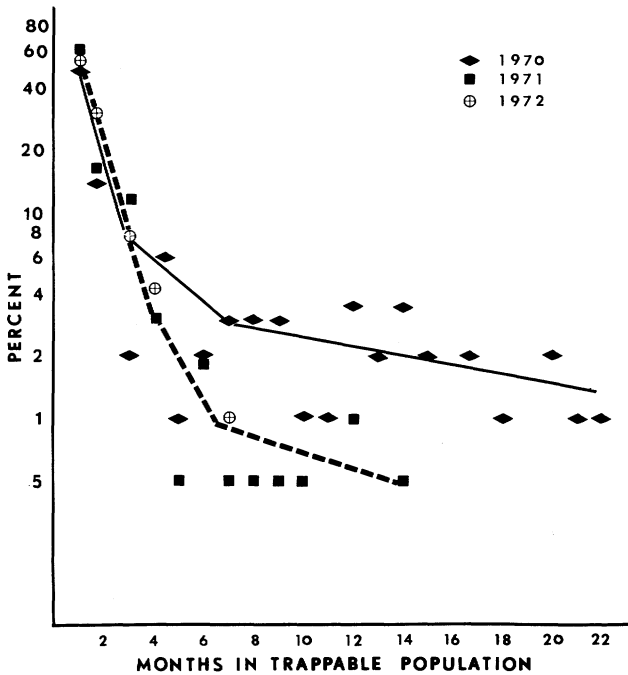
Fig. 5.—Comparison of the percent of juvenile *Dipodomys merriami* recruited into the playa population remaining in the trappable population through time. Insufficient numbers of recaptures of juveniles recruited during 1973–1974 did not allow extension of the data for the 1972 chart.

Perognathus penicillatus was a resident of both the playa and bajada. *Perognathus intermedius* was a resident of the bajada only (Fig. 6). Except for 1973, densities of *P. penicillatus* were higher on the playa than bajada. *P. intermedius* populations were lower than *P. penicillatus* populations on the bajada until autumn 1971. During the drought, *P. penicillatus* density decreased to approximately one per ha and *P. intermedius* maintained the higher densities of the two species until the wetter conditions in 1973, apparently favoring the *P. penicillatus*, reversed this situation. *Perognathus intermedius* was taken on the playa only twice as a transient.

Peromyscus populations increased rapidly in response to available moisture and the availability of succulent vegetation and/or insects (Fig. 7). On the playa *Peromyscus maniculatus* was the only species taken and it was essentially restricted to the grassy playa and immediate fringe until 1973 when two other *Peromyscus* species became established. Recovery of the *P. maniculatus* population exhibited a lag of approximately 6 months following the onset of favorable environmental conditions.

Following the 6 months of wet, favorable conditions in 1973, *Peromyscus* sp. increased on both the playa and bajada. On the playa, populations of
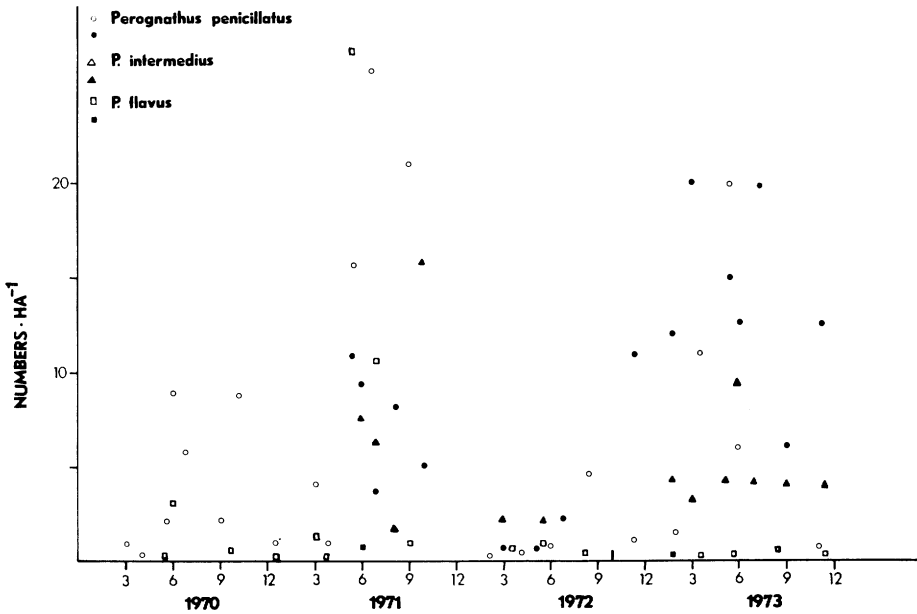
Fig. 6.—Population fluctuations in three species of *Perognathus*. Open symbols are data from the playa and closed symbols data from the bajada.

Peromyscus leucopus and *Peromyscus eremicus* became established and increased in numbers. This increase in both species number and animals density resulted in total densities of *Peromyscus* sp. approaching or exceeding the density of the normally more numerous *Dipodomys* species. The *Peromyscus* during this period were established over the entire area not just the playa bottom.

Until late winter 1972 and 1973, the only *Peromyscus* established as a resident species on the bajada was *P. eremicus*. In 1973 the increase in numbers of resident species and density of *Peromyscus* on the bajada was even more dramatic than that recorded on the playa, with *Peromyscus* sp. supplanting the heteromyids as the most numerous rodents.

Two species, *Sigmodon hispidus* and *Reithrodontomys megalotis*, were restricted to the tobosa grass swales and dense grass of the playa bottom. These species showed little change in population numbers either in 1970 following playa flooding or during the drought of 1971. In 1972, *S. hispidus* populations increased markedly reaching a peak of 40 per ha during 1973 (Fig. 8). *Reithrodontomys megalotis* did not exhibit a marked increase until 1973 then reached a peak of over 60 per ha in September 1973. Coincident with that peak, *R. megalotis* were taken on the bajada, but only during one sampling period in the late summer of 1973. The decreasing populations of both species in the winter of 1973 corresponded with dry conditions and a
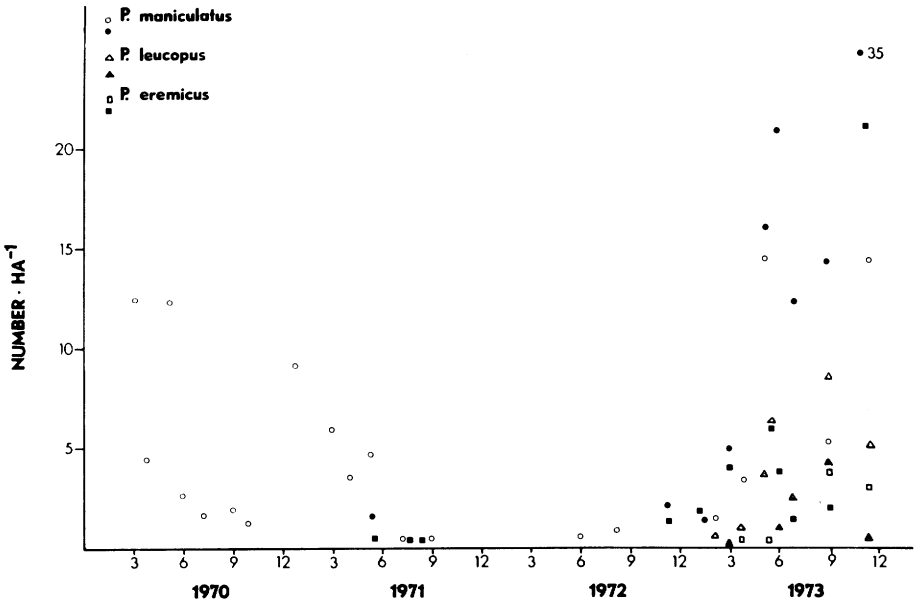
Fig. 7.—Population fluctuations in three species of *Peromyscus*. Open symbols are data from the playa and closed symbols data from the bajada.

reduction in the amount of green vegetation from 2053 kg per ha in the autumn of 1973 to 3 kg per ha in the spring of 1974. Under nondrought conditions, for example, autumn of 1972–spring 1973, green vegetative biomass changed from 1224 kg per ha to 219 kg per ha.

Woodrats (*Neotoma albigula* and *Neotoma micropus*) maintained nearly constant population densities during the entire study period. Because of overlap in diagnostic characters, separation of the two species in the field was not possible although we know from kill trapping that both *N. albigula* and *N. micropus* occur in the same area. The data for *Neotoma* sp. were combined. On the playa, *Neotoma* sp. maintained populations of approximately one per ha. Density estimates of *Neotoma* fluctuated more on the bajada where semiadult animals remained in the trappable population for as long as two to three months. Bajada densities remained constant at about two per ha from 1971 to June of 1973, when the density increased to eight per ha as a number of subadult animals entered the population.

Spermophilis spilosoma is a permanent member of the playa fringe community but was only taken in the spring and autumn when moderate temperatures allowed us to open traps in the early afternoon and then check the traps several hours after sunrise. This species was never taken on the bajada. *S. spilosoma* maintained densities of two per ha until 1973 when densities increased to three per ha. This increase was established adults because all animals taken in April were in breeding condition.
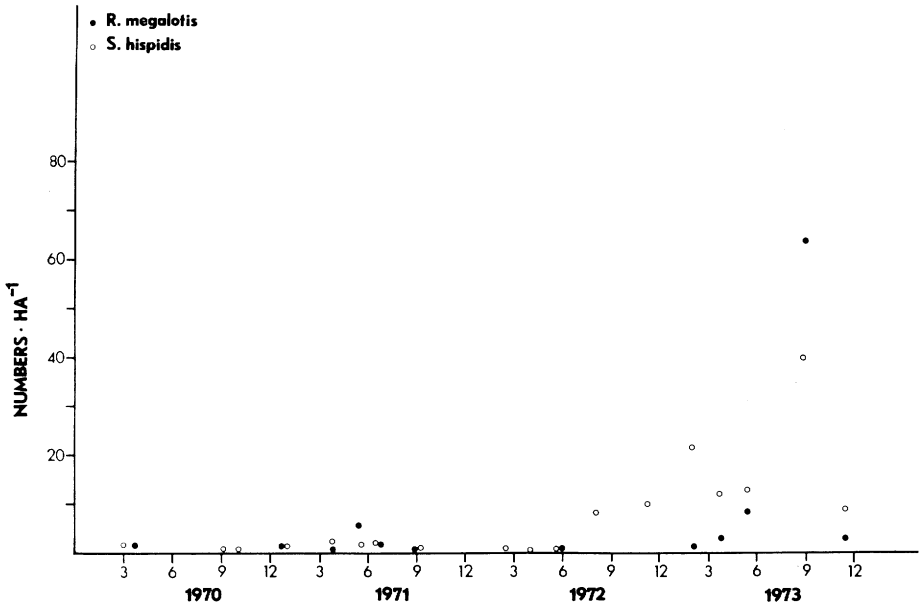
Fig. 8.—Population fluctuations in *Sigmodon hispidus* and *Reithrodontomys megalotis* on the playa site.

Onychomys torridus was recorded at densities varying from 0.2 to 0.4 per ha during the spring and autumn 1970. On the playa estimated densities varied from 0.2 to 0.6 per ha through 1971 and 1972 and increased to 0.9 per ha in 1973. On the bajada *O. torridus* was present during the summer, 1971, at 0.6 per ha but was not taken again until July 1972, when we estimated the population at the same level. In 1973 the population increased from 1.8 per ha in February to 7.0 per ha in September and November and exhibited recruitment in both spring and late summer 1973 (Table 3).

Mus musculus became established on the playa in August 1972 and remained until the end of the study at densities between 0.2 per ha to 0.4 per ha. It was never taken on the bajada.

The yearly shifts in species composition and density can best be understood by comparing the rodent communities prior to peak recruitment in April or May of each year (Fig. 9). Within a single year, 1972, the species diversity index (H′) doubled. When comparisons of H′ are made for the same month in different years, H′ nearly doubled between 1971 and 1973 (Table 2).

The reproductive patterns of the various species are important to an understanding of the changes in density and composition of these communities. In order to compare the reproductive activities of all species, I chose to
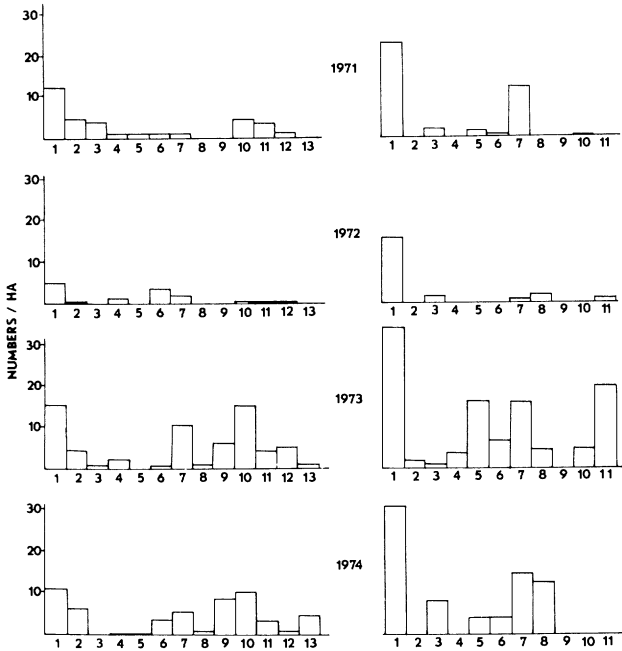
Fig. 9.—Comparison of prebreeding species densities from 1971 to 1974. Data from May dates. Data from the playa site are density estimates based on entire trapping grids uncorrected for habitat suitability. The data on the left are for the playa and on the right for the bajada. Species codes are as follows: Playa—(1) *Dipodomys merriami*, (2) *Dipodomys ordii*, (3) *Dipodomys spectabilis*, (4) *Neotoma* sp., (5) *Onychomys torridus*, (6) *Perognathus flavus*, (7) *Perognathus penicillatus*, (8) *Peromyscus eremicus*, (9) *Peromyscus leucopus*, (10) *Peromyscus maniculatus*, (11) *Reithrodontomys megalotis*, (12) *Sigmodon hispidus*, (13) *Spermophilis spilosoma*; Bajada—(1) *Dipodomys merriami*, (2) *Dipodomys ordii*, (3) *Neotoma* sp., (4) *Peromyscus leucopus*, (5) *Peromyscus maniculatus*, (6) *Peromyscus eremicus*, (7) *Perognathus penicillatus*, (8) *Perognathus intermedius*, (9) *Perognathus flavus*, (10) *Onychomys torridus*, (11) *Reithrodontomys megalotis*.

present the data for 1973 (Table 3 and 4). The reproductive patterns were similar in the other years, however, many species were represented by few individuals in the other years so data on the less abundant species must be interpreted with caution.

DISCUSSION

When the results of this study are examined in the context of previous emperical and theoretical work on species diversity and rodent communities, some significant relationships emerge. Brown (1973) found that the diversity of the seed-eating rodent fauna in sand dune habitats was most closely correlated with the predictable amount of annual rainfall, the best available estimate of the abundance of seeds. My data show that changes in species

TABLE 2.—*Changes in the species diversity index (H') for the rodent population on the playa and bajada 1970–1973.*

Year and location	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1970												
Playa			1.0	1.1	1.2	1.7	1.3		1.3	1.4		
1971												
Playa	1.6		1.6	1.9	1.7		1.5		1.3			0.4
Bajada					1.1	1.1	0.96	0.95		0.99		
1972												
Playa		0.6		1.1		1.6		1.5			1.3	
Bajada	0.36		0.95		0.73		0.91				1.3	
1973												
Playa		1.3		1.9	2.0				1.9		1.8	
Bajada		1.4	1.4		1.9	1.8	1.8		2.0		1.8	

diversity of rodent communities in time was correlated with rainfall and productivity. Brown (1973) points out that numerous studies have reported correlations between species diversity and some aspect of habitat structure, but that in most studies the abundance and predictability of resources was not measured. Rosenzweig and Winakur (1969) suggested that rodent species diversity was related to foliage height diversity, vegetation density, and soil strength. Of these variables, vegetation density, which changed dramatically when high rainfall during the growing season stimulated a flush growth of annual and perennial forbs and grasses was the only one of these related to change in species diversity in my studies. This study and that of Brown (1973) suggest that the relationship between foliage height diversity

TABLE 3.—*Percent of the females captured that were in reproductive condition—pregnant or lactating—during 1973. The data are averaged for the playa and bajada during those months that both sites were trapped.*

Species	F	M	A	M	J	J	A	S	O	N
Dipodomys merriami	35	48	57	52	36	6		7		—
Dipodomys ordii				60				33		
Onychomys torridus	33	40		50						
Perognathus intermedius				50						
Perognathus penicillatus	33	33	20	66		30		33		
Peromyscus eremicus		50		100	33					
Peromyscus leucopus				50				29		
Peromyscus maniculatus		100		50				50		
Reithrodontomys megalotis				33				80		
Sigmodon hispidus	14	100		38				26		

TABLE 4.—*Percent of the individuals captured that were classified as juveniles based on weight and pelage during 1973.*

Species	F	M	A	M	J	J	A	S	O	N
Dipodomys merriami	4	5	3	3	22	22		22		
Dipodomys ordii					20			9		
Onychomys torridus		40		16	50	50		25		
Perognathus intermedius					16					
Perognathus penicillatus					30					
Peromyscus eremicus	50				50			33		
Peromyscus leucopus				23	50			15	6	
Peromyscus maniculatus		33		50	55			17	75	
Reithrodontomys megalotis					25			34		
Sigmodon hispidus		15		33				50	64	

and seed production should be examined to evaluate general importance of resource abundance as a determinant of rodent species diversity.

The generalization that desert rodents, even closely related species, select different habitats (Rosenzweig and Winakur, 1969; Rosenzweig, 1973; Schroder and Rosenzweig, 1975) is supported by the results of this study. The degree of habitat selection and the habitat requirements of individual species is presented in a later section.

The processes resulting in change in species composition and diversity are colonization and extinction, plus moderate change in density of "resident" species. The role of these processes in the establishment of insular faunas is detailed in MacArthur and Wilson (1967) and MacArthur (1972). During a drought period many of the cricetids disappeared from the study area, probably as a result of the disappearance of suitable habitat. During a wet period, a number of species immigrated into the study area and established breeding populations.

Considering the study areas as habitat islands allows comparison of the role of colonization and extinction in structuring the mammal community in local areas with these processes on islands. During wet periods one type of habitat increased greatly (forbs and grasses, plus the seeds they produce and arthropods which feed on these plants) but this habitat was virtually absent during drought (Fig. 10). Thus, during wet periods the island size (habitat) suitable for cricetids increases dramatically. According to the theory of MacArthur and Wilson, increase in island size should result in higher species diversity due to immigration with the time course of such change dependent on the distance from a source area. Conversely, if island size is decreased, as happens during drought, extinction occurs and the species diversity is reduced.

The rapid influx of immigrant species following the onset of favorable growing conditions is probably a function of the proximity of the study watershed to the more mesic refugia of such species. In September 1973,
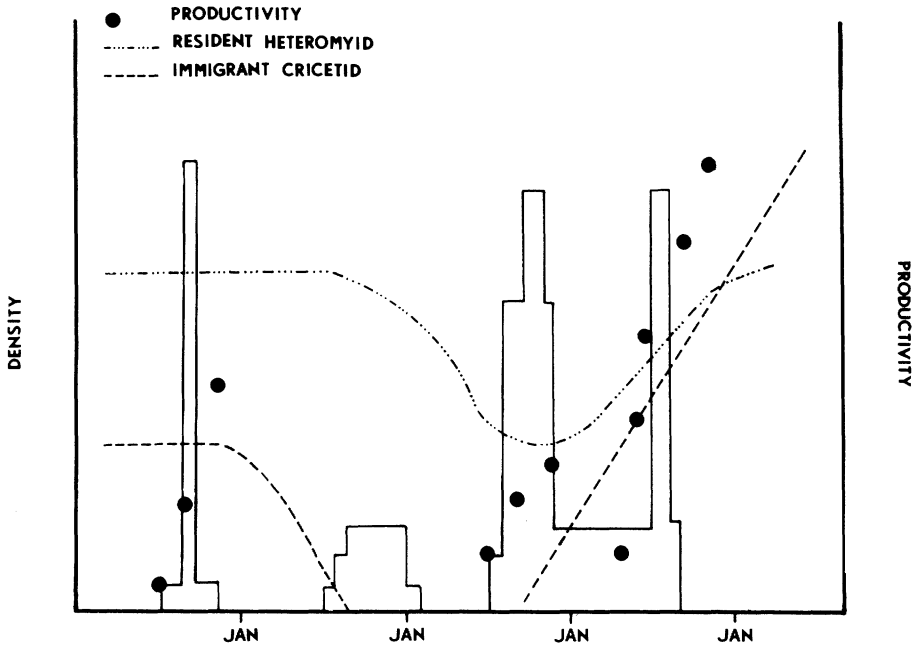
FIG. 10.—A generalized scheme showing the relationship between rainfall (the bar-graphs) productivity and changes in population density of resident heteromyids and im-migrant cricetids.

we trapped a creosotebush flatland which was over 10 km from the nearest mountain which I thought could provide more mesic habitat during drought. The rodent densities were as follows: *D. merriami*, 24 per ha; *D. ordii*, five per ha; *P. flavus*, 13 per ha; *P. penicillatus*, six per ha; *N. micropus*, one per ha; *R. megalotis*, four per ha. The area distant from a mesic re-fugia lacked several species which were abundant on the study area. Also, *P. maniculatus* density was considerably lower on the distant area. These data support the premise that distance from principal habitats and immigra-tion were important factors affecting the rapid change in species composi-tion on the Validation Site. The changes in these rodent communities are those of a "habitat island" fauna subject to immigration and extinction even though the "islands" are part of a contiguous watershed.

The dynamics of "resident" and immigrant species are in large part a function of the breeding periods and reproductive potentials of these species. Based on literature reports, the average number of embryos per female in the heteromyids and cricetids is as follows: *D. merriami*, 2.0; *D. ordii*, 2.4; *P. penicillatus*, 3.5; *P. leucopus*, 7.0; *P. eremicus*, 3.1; *P. maniculatus*, 4.5; *R. megalotis*, 3.8; *S. hispidus*, 3.4 (Baccus, 1971; Reynolds, 1960; Johnston, 1956). The resident heteromyids not only have lower reproductive potentials

than the *Peromyscus* species which were the most important immigrants but my data show breeding and recruitment of young in *Peromyscus* sp. throughout the year. Although *Dipodomys* sp. and *Perognathus* sp. may produce more than one litter in a year, the higher reproductive potential and what appears to be a continuous breeding season in *Peromyscus* results in a more rapid increase in numbers. Such reproductive characteristics make it possible for *Peromyscus* sp. to rapidly attain high densities in habitats which are only periodically suitable (Fig. 10). High reproductive output allows these species to exploit resources before the populations of resident heteromyids increase and compete for food with cricetids. *R. megalotis* and *S. hispidus* also have reproductive characteristics which allow rapid response to resources which vary greatly and unpredictably. However, they are limited by habitat requirements and do not become established in habitats preferred by the other species.

Differences in species composition and animal densities between playa and bajada resulted from the interactions of "resident" species, that is, those species which inhabit the area even under the most severe environmental conditions with the immigrants from a "source area," in this case, the probably more mesic Mt. Summerford. I will discuss those factors which effect the dynamics of "resident" species first, before considering the "immigrant" species.

The "residents" of the playa fringe (mesquite, mormon tea-yucca association) are primarily the heteromyids—*D. merriami, P. penicillatus, D. ordii,* and the habitat-limited *Neotoma* sp. The heteromyids are able to survive drought periods probably by using cached seeds. They actually exhibited population increase during early summer 1971, despite the virtual absence of green forbs and grasses and insects, suggesting that survivorship and recruitment of these heteromyids is a function of caloric content of forage and not on its succulence as suggested by Bradley and Mauer (1971) for Mojave Desert heteromyids.

The ability of these species to survive on metabolic water (Schmidt-Nielsen and Schmidt-Nielsen, 1951) when sufficient food is available allows survival during drought periods. The population crash exhibited by the heteromyids between 1971 and early summer 1972, resulted from the low survivorship of the young recruited in 1971 in comparison to those recruited in 1970. Survivorship may be strongly influenced by seed availability and subsequent caching. If seed caching by young animals is difficult, the increased time spent foraging and their possible weakened conditions could make such animals more prone to predation than would be individuals who have seed caches to exploit.

Woodrats (*Neotoma* sp.) in the Chihuahuan Desert appear to be habitat limited in the sense described by Brown *et al.* (1972). Around the playa fringe, woodrats build nests in the base of large clumps of mesquite (*Prosopis glandulosa*). Only those clumps greater than 3 m in diameter, with stems

in excess of 2 m height were inhabited by *Neotoma*. Around the playa, *Neotoma* fed on the green leaves of *Yucca elata* and during drought periods removed bark from the stems of *Prosopis*. On the bajada *Neotoma* nested in the middle of large clumps of *Yucca baccata* using the leaves as nest building material, and also in the large clumps of Apache plume, *Fallugia paradoxa*, which lined the arroyos. The increase in *Neotoma* population on the bajada was due entirely to young animals building nests in the *Fallugia* thickets along the arroyo. *Fallugia* exhibited considerable new growth in 1972 and 1973 which probably increased its suitability as *Neotoma* habitat. The dependence of woodrats on these limited habitats supports the conclusions of Brown *et al.* (1972) that the habitat provides most of the resources required—food, water, materials for den construction, and means of avoiding predation (for example, mesquite bark is succulent all year as are the leaves of *Yucca*; mesquite, *Yucca* and *Fallugia*, provide thick spinous deterrents to predators attempting to get at a den and provide spiny materials for den construction).

Two other species which were limited by habitat were the western harvest mouse, *R. megalotis*, and the cotton rat, *S. hispidus*. Cattle grazed the playa during 1970 and 1971 reducing grass cover to small areas of tobosa grass swale and mixed *Panicum*. Cattle were excluded in 1972 and the high productivity resulted in nearly complete grass cover over the playa from July 1972 through 1973. The increases in *S. hispidus* and *R. megalotis* were coincident with the increased cover and the maintenance of green vegetative parts of both *Panicum* and *Hilaria* through the winter and early spring of 1972–1973. Fleharty and Mares (1973) reported that *S. hispidus* preferred habitats with dense undergrowth and protective overstory. Such habitats were limited to less than one/ha under grazing, but increased to greater than 14/ha when protected from grazing by cattle.

Perognathus flavus appeared adversely affected by protection of the playa grassland from grazing. *Perognathus flavus* were taken in highest densities in the areas of the playa with the sparsest grass cover where grazing and trampling had been concentrated. When grazing was eliminated and grass cover of the bottom complete, *P. flavus* remained a marginal, low density species. This suggests that *P. flavus* require sparse or clumped grass cover with considerable open spaces to establish high population densities.

Spermophilus spilosoma responded to increased productivity directly. *Spermophilis spilosoma* feeds on a mixed diet of seeds, vegetative parts, and insects. Increased production in 1972 evidently increased successful recruitment of young ground squirrels which survived and reproduced in spring 1973 producing the marked increase in ground squirrel numbers in 1973.

Although *O. torridus* was taken in nearly every sampling period on the bajada, its population did not change significantly until plant production increased in 1972 and 1973. *Onychomys torridus* exhibited a lag in its population increase similar to that exhibited by the heteromyids, hence, it ap-

peared to be responding to increased food availability through increased success in recruitment, but with the attendant delay imposed by recruitment and establishment of young in the population.

Peromyscus maniculatus exhibited some characteristics of a resident on the playa but was not trapped during the drought hence will be considered as an immigrant in this paper. *Peromyscus eremicus* was a resident of the bajada which exhibited a response similar to *O. torridus* but because of its reproductive potential increased at a faster rate in response to increased productivity.

It is evident that resident species responded to increased primary production by increased recruitment and increased survivorship. Those species which are habitat limited either did not respond to the increased production or did so only in cases where increased habitat became available. Changes in habitat structure due to change in management practices apparently were as important in effecting densities of cotton rats, harvest mice, and silky pocket mice as the changes in productivity.

Fluctuations in population densities of immigrant species can result from two interacting and inseparable processes. Above average precipitation and production leads to increased recruitment into populations of *Peromyscus* (Table 1) and also increases the area of suitable habitat.

The appearance of *R. megalotis* and *D. ordii* on the bajada were coincident with peak population and recruitment of the playa. Hence, these immigrants were probably the result of high density intraspecific interactions forcing high rates of emigration from the preferred habitat areas of the playa.

The disappearance of *Peromyscus* from the playa in 1971 probably resulted in large part from change in habitat suitability. Above average rainfall produced habitat suitable for *Peromyscus* sp. over the entire study area. Potential refuges for *P. leucopus*, *P. maniculatus*, and *P. eremicus* during periods of low rainfall and productivity are the north facing slopes of Mt. Summerford, 2 to 3 km from the study sites. These slopes support scattered junipers and other vegetation characteristic of areas more mesic than the playa and bajada. As the populations of *Peromyscus* increased rapidly in the more mesic areas, intrapopulation pressure would force immigrants into other areas where these animals would either find habitat suitable for establishing a breeding population or become extinct. These relationships are similar to the observations of Brown (1975) that on a geographic scale the cricetids *Peromyscus* and *Reithrodontomys* are only present in desert habitats where productivity is high and/or potentially competitive heteromyids are absent because of biogeographic barriers to their dispersal. Hoover (1973) has demonstrated that *P. intermedius* is capable of expanding its range and competing with *P. penicillatus* when moist conditions prevail but is forced to retreat to the more mesic mountain sides during drought periods. Thus, immigrant species are provided with greatly enlarged habitat areas and

conditions favorable for greater survivorship during wet periods and in areas similar to our study areas, can exceed the densities of permanent residents.

The dynamics of Chihuahuan Desert rodent communities can be summarized as follows. Drought conditions reduce species diversity due to resource limitation which results in lower density and may result in the local extinction of some of the more mesic adapted species such as *P. leucopus*. Reduced densities in resident species result from lower survivorship of young. A succession of wet years with high plant production results in increased species diversity and higher densities primarily due to increased habitat area suitable for immigrant species to establish populations. Resident species exhibit lags in population response to favorable conditions due to lower reproduction and recruitment rates than immigrant species. Immigration and extinction causes rapid changes in species diversity correlated with changes in productivity.

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