THE LONG-TERM EFFECTS OF HABITAT MODIFICATION ON A DESERT RODENT COMMUNITY

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Abstract.—Data are presented from the results of a 14-year study of changes in composition of a desert rodent community following habitat perturbation. We studied rodent populations in an area where herbicide treatment reduced shrub cover from 16.7 percent to less than one percent and increased grass cover from 1.3 percent to 22.3 percent. In the first two years following the perturbation, *Dipodomys ordii* was the most abundant rodent in the grass habitat, whereas *D. merriami* remained the most abundant species in the shrub habitat. From 1976 through 1984, the rodent community in both areas was dominated by *D. merriami* and *D. ordii* was absent or occurred at low densities in both habitats. Species richness was highest in 1976 and 1985 following successive "wet" seasons. In 1985, following three above average wet seasons, *D. ordii* once again became the most abundant rodent in the grass habitat. *Neotoma micropus* increased in abundance with increased grass cover. These results suggest interspecific competition between *D. ordii* and *D. merriami* during average to dry periods of limited resources. Successive wet seasons allow *D. ordii*, which has higher fecundity, to increase because resources are not limiting during such periods. Successive wet seasons result in increased species richness due to immigration of opportunistic species like *Sigmodon hispidus* and *Reithrodontomys megalotis*.

Numerous studies of rodent communities have emphasized the relationships between characteristics of vegetation such as species composition, percent cover, and foliage height and the diversities, densities, and species compositions of the rodent assemblages (Allred and Beck, 1963; Rosenzweig and Winakur, 1969; Brown, 1973; Hallett, 1982). Several studies have utilized field manipulations of the habitat to examine responses of rodent species composition to marked habitat modification (Rosenzweig, 1973; Price, 1978; Holbrook, 1979; Parmenter and MacMahon, 1983). Such studies of habitat use characteristically are conducted for less than one year to as long as three years. They provide documentation of the changes in rodent communities resulting from the change in vegetation architecture, microclimate, or food but provide no data on the stability of the resultant rodent community nor insights into which parameters are the most important in structuring the assemblage.

As part of the US/IBP Desert biome studies, we studied changes in vegetation and rodent communities resulting from the habitat modification of shrub removal by herbicide treatment. The rapid increase in grass cover and initial changes in the rodent community were reported in Whitford *et al.* (1978). We continued to sample the treated area and an adjacent untreated shrub habitat from the end of that program in 1974 to the present in order to study the stability of the differences in rodent community structure through time. Data were not collected in 1978, 1982, and 1983. If differences in structure of the rodent communities on the herbicide treated

and untreated areas were the result of vegetation architectural differences, then the species rankings should remain relatively constant through time providing the vegetation structure remained relatively constant.

STUDY AREA AND CLIMATE

The study site was an 18-hectare area approximately five kilometers east of the Desert Biome Jornada Site, which is 40 km. NNE Las Cruces, Dona Ana County, New Mexico. The site is part of the drainage of the watershed on which the Jornada Site is located (Whitford, 1976). The study site was located at the lower end of the alluvial fan of the Dona Ana Mountains. Soils were sandy loam alluvia, and supported a Chihuahuan desert shrub community. The soil composition was as follows: stones greater than two millimeters in diameter made up 16 percent of the weight; the remaining soil fraction was 63 percent sand, 16 percent silt, and 21 percent clay by volume. Soils were the same on the treated and untreated areas.

The 75-year average annual rainfall for this area is 211 millimeters (Houghton, 1972) with most of that rainfall occurring in late summer convectional storms. Summer maximum air temperatures regularly reach 38° to 40°C. Temperatures below freezing are recorded between October and April.

Data from the pretreatment census of rodents on the area that was subjected to herbicide treatment and the adjacent area used a control showed no differences between the areas (Whitford *et al.*, 1978). Although we used only one grid per area, we are confident that the data represent responses of the mammal communities to the habitat changes and climatic conditions of the period of studies. Before the area was divided into a control and treatment sprayed with herbicide, it was a shrub desert with a total shrub cover of 16.7 percent. Creosotebush, *Larrea tridentata*, accounted for 57 percent of the shrub cover (Whitford *et al.*, 1978). Nine hectares were treated with the herbicide dicamba applied at the rate of 2.5 kg. · ha^{-1} in September 1971 and September 1972. The herbicide killed most of the woody shrubs (Fig. 1). Within two years of the herbicide application, grass cover had increased from 1.3 percent to 8.6 percent primarily due to the increased diameters of pretreatment clumps of *Mullenbergia porteri* and *Hilaria mutica*. Between 1975 and 1984, grass cover increased to 22.3 percent and shrub cover to 1.8 percent. From 1975 to the present, there has been little recovery of shrubs on the treated area but the grass cover has increased to more than 16 percent (Fig. 1). In 1975, the trapping grid on the shrub habitat had a total vegetative cover of 14.1 percent: 10.4 percent shrub cover and 3.7 percent grass cover. In 1984 and 1985, the shrub habitat grid had 10.4 percent shrub cover and 4.6 percent grass cover. Snakeweed, *Xanthocephalum* sp., accounted for only 0.6 percent of the vegetative cover in the shrub habitat throughout the study period.
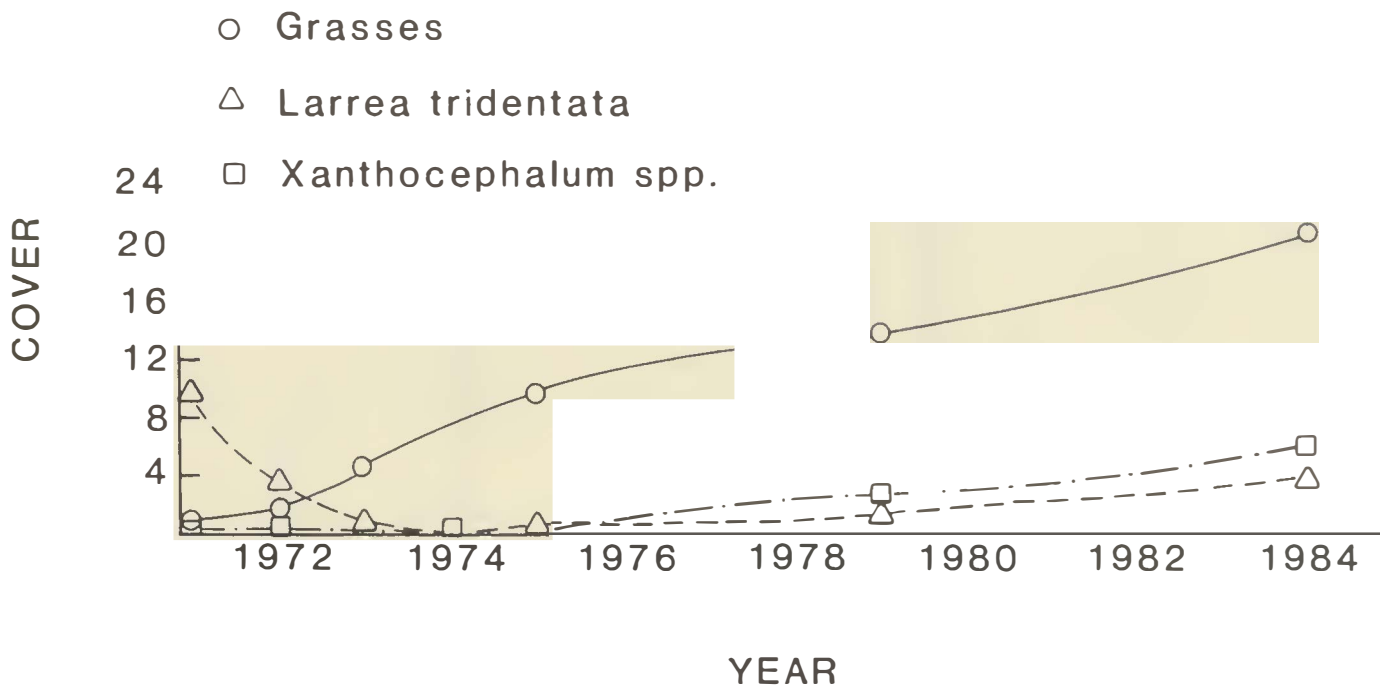
FIG. 1.—Changes in percent cover of grasses and shrubs; recovery of the shrub *Larrea tridentata*, and increases in grass and snakeweed, *Xanthocephalum* sp. on the study area treated with the herbicide dicamba (to kill woody perennials) in 1971 and 1972.

METHODS

Rodents were sampled over four consecutive nights in mid-summer or early autumn. The grass and shrub habitats were trapped simultaneously. Sherman live-traps baited with cracked milo or mixed seeds were set on grids of 100 by 100 meters, 100 stations, 10 meters trap spacing. On several sampling dates in 1975, we used assessment lines to obtain data on the effective grid size for use in density computations. The trapping grid for the herbicide-treated grass habitat was placed in the center of that area. The shrub habitat grid was placed 50 meters east of the herbicide-treated area. Traps were checked at dawn; trapped animals were marked by toe clipping and released. Population densities were estimated by the Lincoln Index. When insufficient numbers of marked animals were captured to provide an accurate Lincoln Index estimate, the total number of different individuals captured over the four-night period was used as the estimate of the population density.

Vegetation cover was estimated by running a series of line intercepts down the trap lines in both the grass habitat and shrub habitat sites.

RESULTS

In the years immediately following the herbicide treatment, the rodent community structure changed with *Dipodomys ordii* replacing *D. merriami* as the most abundant large heteromyid on the area that had increased grass cover and decreased shrub cover (Fig. 2). However, within four years after herbicide treatment, the *merriami* to *ordii* ratio was 2:1 in the grass habitat as compared with a 5:1 *merriami* to *ordii* ratio on the shrub area (untreated
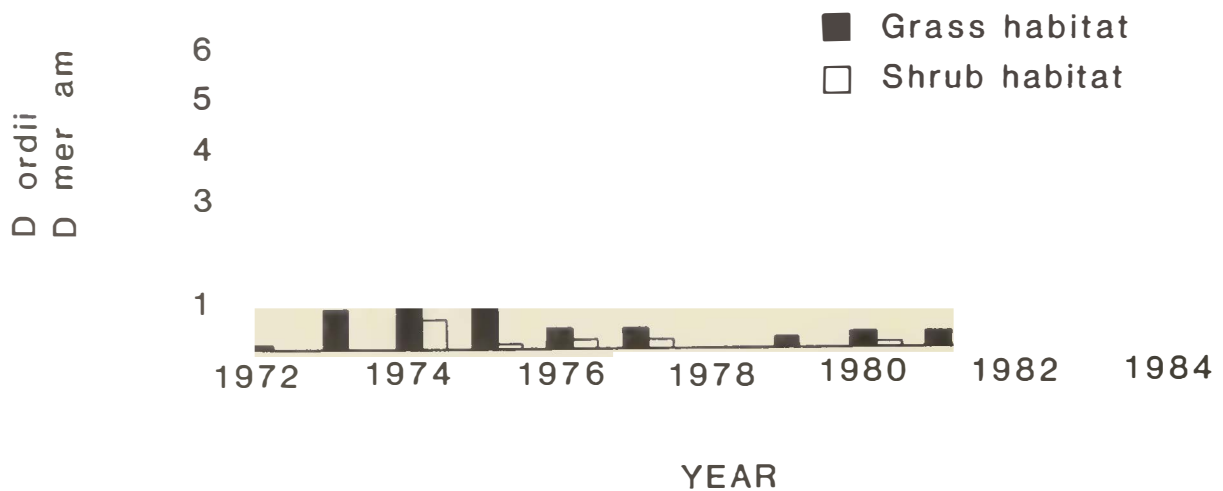
FIG. 2.—Variation in the ratio of *D. ordii*, *D. merriami* densities in a herbicide-induced grass habitat and adjacent shrub habitat.

control) (Fig. 2). By 1979, the *merriami* to *ordii* ratio had changed to 4:1 on the grass area and in 1980 was 4:1 for the grass habitat and 9:1 for the shrub habitat. Thus during the years 1976 to 1984, *D. merriami* was more abundant than *D. ordii* in both the grass and shrub habitats (Fig. 2). Densities of desert rodents were extremely low in 1984, not only on the study area but also on other areas in the vicinity. In July-August 1985, the ratio of *ordii* to *merriami* was greater than 1.0 in the grass habitat and 0.8 in the shrub habitat (Fig. 2).

Rainfall during the study was separated by season, that is, predictable rain season (July-October), season of variable precipitation and below freezing temperatures (November-March), and dry hot season (April-June). The first shift in *ordii* to *merriami* followed three years of above-average summer or winter precipitation, or both, that resulted in exceptionally high herbaceous plant production (Fig. 3). The years between 1975 and 1984-85 generally were characterized by occasional above average wet seasons preceded and followed by dry seasons. In 1984-85, there were three consecutive above average wet seasons (Fig. 3) that were followed by a second shift in *ordii* to *merriami* ratios (Fig. 2) and increased rodent density and species richness (Table 1).

Total rodent densities were exceptionally high in 1976, then dropped to 29 · hectare^{-1} in the grass habitat and 17 · hectare^{-1} in the shrub habitat in 1977; moderate population levels, ranging from 33 · hectare^{-1} to as low as 7.1 · hectare^{-1} in the shrub habitat in 1979 (Table 1) occurred during the remainder of the study. Species richness was highest in 1976 and 1985 with seven and eight species, respectively, in the communities during those years (Table 1). There has been an increase in *Neotoma micropus* in the grass habitat and variable but low numbers of *N. micropus* or *N. albigula* in the shrub habitat. In 1985, there was a newly established mound of *D. spectabilis* at one edge of the trapping grid in the grass habitat (Table 1).
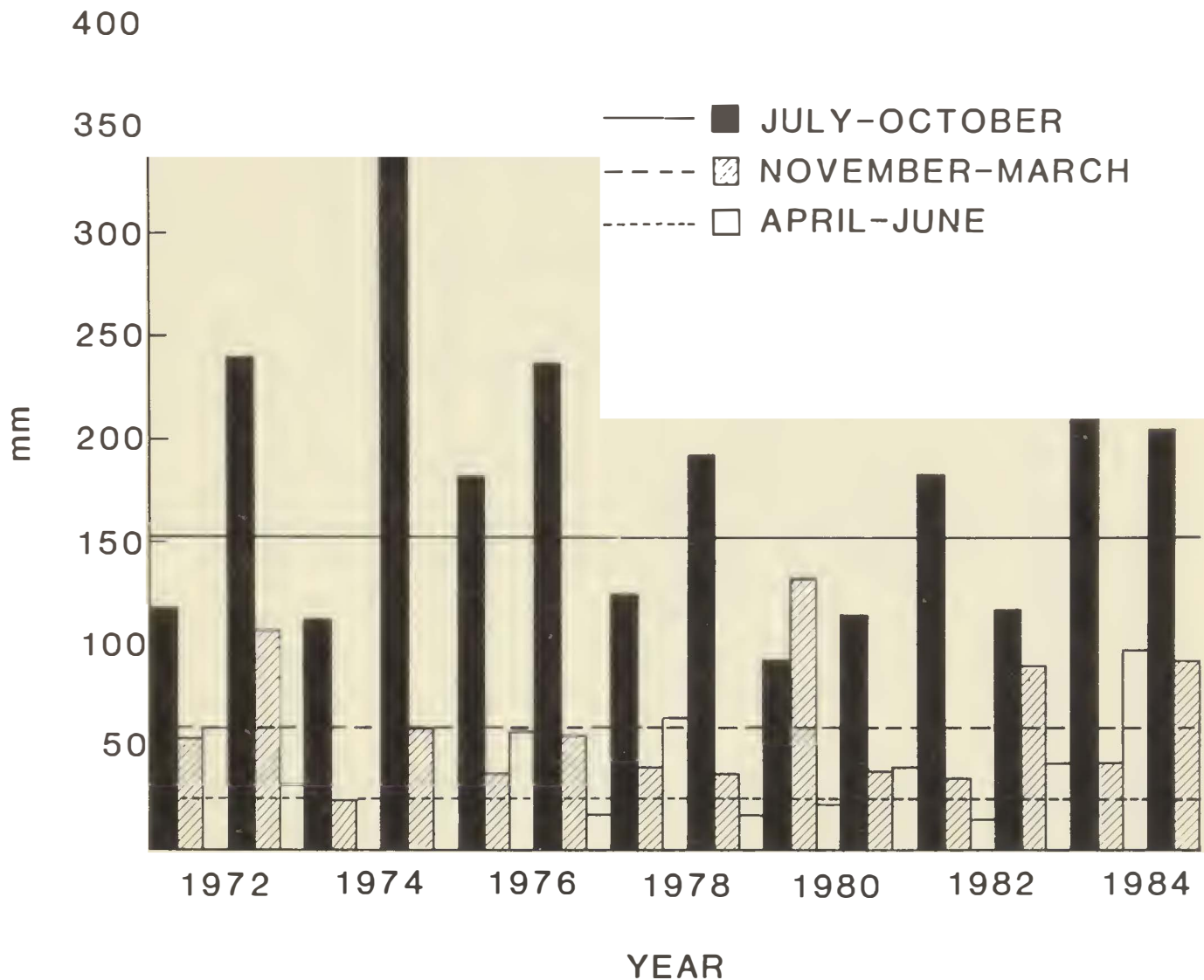
Fig. 3.—Total rainfall by season at recording stations within 10 kilometers of the study site from 1971 through March 1985. Horizontal lines indicate the long-term average precipitation for the rainfall seasons.

Discussion

It was fortuitous that in the 10 years since we reported a replacement of *D. merriami* by *D. ordii* as the most numerous rodent in this community that favorable climatic conditions produced a repeat of this condition. The complete absence of *D. ordii* from the control plot during some years and the continued presence of this species in the grassier habitat supports contentions that *D. ordii* is found in grassier habitats (Shroder and Rosenzweig, 1975). Apparently, when the more typical northern Chihuahuan desert climate prevails, *D. ordii* continues to occur at low densities in the grassland habitat. The climatic conditions that allowed for large increases in *D. ordii* populations in the general area apparently included successive wet seasons and a good crop of winter annuals in the spring preceeding the "boom" or exceptionally wet summer and early autumn.

These data provide some insights into the potential competition between *D. merriami* and *D. ordii*. Schroder and Rosenzweig (1975) used a removal experiment to assess competition between these species and concluded that the interspecific alpha was zero. They cautioned this should not be

TABLE 1.—*Estimated densities of desert rodents (number · hectare*$^{-1}$*) on a herbicide treated, desert grassland, shrub removal site (T) and an adjacent untreated shrubland site (C) on sampling dates from October 1976 through July 1985.*

	1976		1977		1979		1980		1981		1984		1985	
	T	C	T	C	T	C	T	C	T	C	T	C	T	C
Dipodomys merriami	46.2	18.9	17.1	12.4	7.6	5.9	8.8	11.8	18.3	18.3	10.7	9.5	7.6	10.1
Dipodomys ordii	20.1	4.7	7.7	2.4	1.8	0.0	2.4	0.6	5.3	0.0	1.2	1.2	9.5	8.9
Perognathus flavus	5.9	0.6	0.0	0.6	0.6	0.0	0.0	1.2	1.2	1.2	0.0	1.8	0.6	3.6
Peromyscus maniculatus	0.6	0.6	0.0	0.0	0.0	0.6	0.6	1.2	1.8	2.9	0.0	2.4	2.4	5.3
Neotoma albigula	0.0	0.6	0.0	0.6	0.0	0.6	0.0	0.6	0.0	0.6	0.0	1.2	0.0	0.6
Neotoma micropus	1.2	0.0	1.2	0.0	0.6	0.0	0.6	0.0	0.6	0.6	1.2	0.6	5.3	1.2
Onychomys arenicola	4.7	0.6	3.0	0.6	0.6	0.0	0.0	0.6	0.0	2.4	0.0	0.6	2.4	3.0
Sigmodon hispidus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6
Reithrodontomys megalotis	1.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dipodomys spectabilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0
Total density	80.5	26.6	29.0	16.6	11.2	7.1	12.4	16.0	27.2	25.4	13.1	17.3	29.6	33.3
Number of species	7	7	4	5	5	3	4	6	5	6	3	7	8	8

interpreted that interspecific competition is unimportant in the system and suggested that were it not for the continual threat of interspecific competition, the habitat specializations would soon disappear. These authors conducted their studies during above average wet years (1972-1973), which resulted in changes in the distribution of *D. ordii*. Considering the Shroder-Rosenzweig studies and our 10-year data set, it is plausible that the results of their removal experiments might have been different in average or dry years. Our 14-year data set (including data in Whitford *et al.*, 1978) is consistent with the arguments of Wiens (1977) that competition between co-existing species may occur primarily under conditions of resource limitation and that competition may be diluted (or nonexistent) during periods of resource abundance. During the more than 10 years of sampling in this study, *D. ordii* was more numerous in the grassier habitat only after more than one year of above-average rainfall and exceptionally high productivity, especially of the annual buckwheats, *Eriogonum* sp. (Whitford 1972, 1973, 1974, and unpublished data from the Jornada LTER Project). If grassier habitats are especially favorable to *D. ordii*, then that species should have maintained population densities close to those of *D. merriami* in that habitat during the intervening average-to-dry series of years. The marked decrease in *D. ordii* during that period suggests that *D. merriami* is behaviorally and physiologically superior to *D. ordii* and is proably out-competing *D. ordii* during the "crunch" years. However, even given that competition, *D. ordii* apparently does better in the grassier habitat than in the desert shrub habitat.

The changes in relative abundance of *D. ordii* and *D. merriami* may be examined with respect to the threshold hypothesis of Conley *et al.* (1977) (Fig. 4A). Conley *et al.* (1977) argued that fluctuations in small mammal populations are not simply a function of climatic variability but rather the result of climatic fluctuations that fall below some threshold level needed to produce the minimum resources for that species. Their graphical model presents a single threshold for a species population and does not account for habitat as a modifier of the climatic effect. The threshold level of resources for a species must be considered as the minimum value for all of the resources of the species niche. Climatic conditions that fail to produce that minimum set of resources result in reduced natality and survivorship. In our modification of the threshold hypothesis, we indicate how habitat can affect resources with respect to the thresholds of the species (Fig. 4B). In this graphical model, the climate threshold for *D. ordii* would be higher in shrub habitat and that of *D. merriami* would be higher in the grass habitat. Variation in climate affects resources such as burrows or den sites, distribution and abundance of seeds, phenology and productivity of herbaceous plants, shrubs, and grasses, and so on. The effect that variation in climate has on resources varies with habitat because vegetative structure, slope, and soil affect water infiltration, run-off, soil water storage, water extraction, nutrient distribution, seed distribution patterns, and seed species
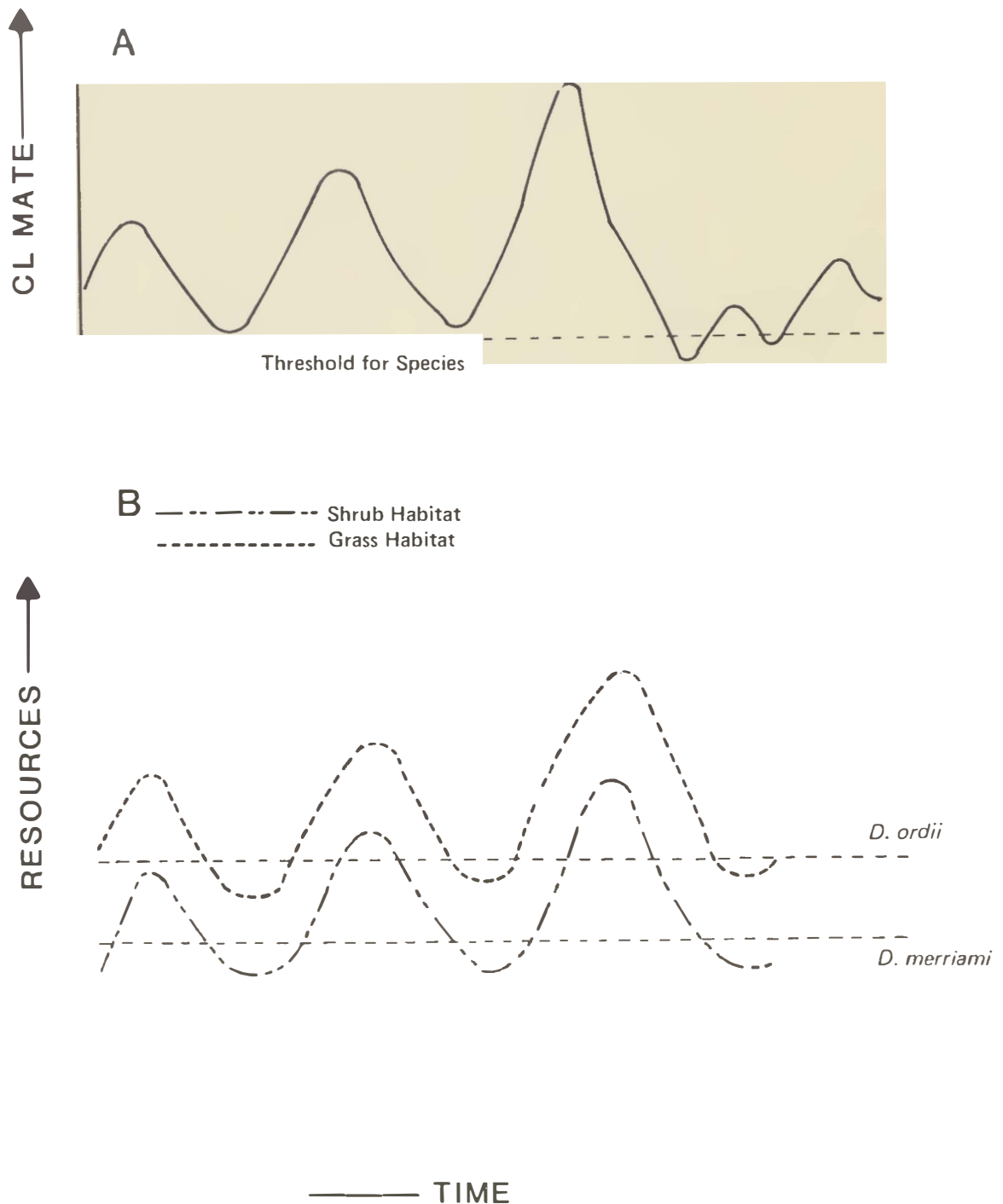
Fig. 4.—The threshold hypothesis of Conley *et al.* (1977) presented in A is compared with the variation in resources in two habitats (B) produced by the climatic fluctuation presented in A. Physiological and behavioral differences of *D. ordii* and *D. merriami* affect the minimum resource threshold for each species.

as examples of resources that are important to desert rodent species. Considering climate-resource thresholds for species and the effects that habitat can have on those resources should help us to make predictions about the structure of rodent communities through time, especially with respect to species that are potential competitors.

Applying that model to the 10-year data set from the Jornada Site provides some useful insights into the changes in rodent community structure in these habitats. If the resource threshold necessary for physiological-behavioral characteristics of *D. ordii* is higher than that of *D.*

merriami, then *D. ordii* will maintain low populations in favorable habitats and drop to zero in less favorable habitats. Under especially favorable conditions, population responses of both species will be a function of natality and survivorship. *D. ordii* has a larger mean litter size (3.16 per female) and larger range in litter size (one to six young per female) than does *D. merriami* (2.49; one to five young per female) (Conley *et al.*, 1977). Whitford (1976) reported that a portion of the females of *D. merriami* were receptive, pregnant, or lactating from February through September with less than 10 percent in reproductive condition in July through September, whereas *D. ordii* exhibited two distinct reproductive periods in May and September. Together these data suggest that under favorable conditions the natality of *D. ordii* is greater than that of *D. merriami*. If several consecutive seasons of above-average wet conditions result in greater natality of *D. ordii*, then several consecutive seasons of dry conditions would result in lower survivorship in comparison to *D. merriami* according to the threshold hypothesis. The physiological-behavior attributes of *D. merriami* that make the climate-resource threshold for that species lower than that of *D. ordii* probably gives *D. merriami* the competitive edge during relatively dry periods. The lower resource threshold of *D. merriami* should allow it to utilize scarce resources, thus further reducing the availability of common resources to *D. ordii*. The reduced availability of resources resulting from climate and competition would reduce both natality and survivorship of *D. ordii*. These relationships are consistent with the long-term data set reported here. Confirmation will require experimental studies of natality and survivorship in these habitats.

These data provide additional evidence for "resident" and "immigrant" or opportunistic species in desert rodent communities. Temporal variation in climate had some effect on population densities of *D. merriami*, *Onychomys arenicola*, *Neotoma* sp., and *Perognathus flavus*, which can be considered permanent or "resident" components of these rodent communities. *Sigmodon hispidus*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus* are occasional or opportunistic members of the community. *D. spectabilis* appears recently to have established dens in the grass habitat and may become a "resident" in that habitat. Consecutive above-average wet seasons or extremely wet summers apparently result in marked increases in certain species of this desert rodent community—*D. ordii*, *Perognathus flavus*, *Peromyscus maniculatus*. Such conditions also facilitate the spread of opportunistic species such as *S. hispidus* and *R. megalotis* into marginal habitats from habitat refugia. (Whitford, 1976).

One species that seemed to be favored by the increase in grass cover was the woodrat, *Neotoma micropus*. Wright (1973) studied the habitat distributions of *Neotoma* species in southern New Mexico and reported that *Neotoma* was not found in *Larrea tridentata* shrub habitats. Whitford (1976) reported *Neotoma* sp. in *L. tridentata* shrub lands associated with small drainages where the rats utilized *Yucca baccata* clumps as den sites. There

was no measurable change in *Yucca* sp. densities in the grass habitat during this study but the increased size of clumps of *Muhlenbergia porteri* around the *Y. baccata* seems to have made these clumps suitable den sites. By 1985, virtually every *Y. baccata* clump in the grass habitat hosted a woodrat den. In the shrub habitat, few of the *Y. baccata* clumps had woodrat dens. Brown *et al.* (1972) suggested that the capacity of a habitat to support woodrats depends upon the extent to which it affords them protection from predators. Dense clumps of *M. porteri* may indeed serve such a function in the man-induced grassland habitat.

This desert rodent community differs from that of other nearby desert rodent assemblages in that two relatively common species, *Perognathus penicillatus* and *Peromyscus eremicus*, never have been taken in this area. These are common species in similar habitats within 10 kilometers of this study site (Whitford, 1976). The absence of an intermediate size heteromyid (*P. penicillatus*) and relatively abundant congeners of virtually the same body size (*D. merriami* and *D. ordii*), makes this assemblage of heteromyids deviate from that predicted by Brown (1975) and discussed by Bowers and Brown (1982). Bowers and Brown (1982) did not include Chihuahuan desert sites in their analysis because there were insufficient localities for independent statistical analysis. Therefore, we cannot be certain that the conclusions of Bowers and Brown (1982) apply to Chihuahuan desert rodent communities. *P. penicillatus* occurs in similar habitats in other areas on the same watershed. Why should *P. penicillatus* not occur in this community? We can only speculate that some combination of habitat features and competition are responsible.

This study demonstrates the value of long-term data sets to obtain insights into community dynamics of rodents. The results of these long-term studies indicate the necessity for caution in assuming habitat specialization as the primary means of competition avoidance by rodents. Long-term studies also suggest important questions and study designs that account for the vagaries of climate. It is likely that some of the controversies and inconsistencies in results of rodent community studies may be resolved only by such long-term studies.

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