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Implications for Conservation of the Species Diversity and Population Dynamics of Small Mammals in an Isolated Reserve in Mexico City

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ABSTRACT: We studied the influence of habitat loss and fragmentation in species diversity, population dynamics, and habitat use in a small mammal community in xeric palo loco (*Senecio praecox*) thickets at Reserva Ecologica del Pedregal de San Angel, a completely isolated nature reserve in Mexico City, Distrito Federal, from 1989 through 1990. It is a heterogeneous region, dominated by an old lava flow, with many boulders and crevices. Small mammals were captured using Sherman live traps in two 0.81-ha grids; each grid contained 10 rows and 10 columns, separated by 10 m. Nine species have disappeared since 1957 as a result of the loss of particular habitat such as grasslands, habitat fragmentation, and other causes. In our study, we recorded nine species; five species were exclusively recorded in the continuous native scrub of the reserve. Therefore, they are good indicators of the sites in the reserve that maintain the less perturbed habitats. Interestingly, no introduced rodents (i.e., roof rat (*Rattus rattus*) and house mouse (*Mus musculus*)) were found in the continuous scrub of the reserve. Only six were caught in our grids (three were relatively common, represented by more than 10 individuals). Reproduction and maximum population densities of all species were very seasonal and peak at time of available high food resources, suggesting that food availability was the limiting factor.

Index terms: community structure, habitat heterogeneity, habitat use, mammal species diversity, *Neotoma mexicana, Peromyscus gratus,* population dynamics, population extinctions

INTRODUCTION

One of the most pervasive consequences of development has been the increasing fragmentation of habitats and ecosystems, resulting in the extinction of many species and populations (Ehrlich and Ehrlich 1981; Global Environmental Assessment 1995; Ceballos and Ehrlich 2002). As fragmentation progresses as a result of anthropogenic activities, the species richness and the long-term dynamics of remaining populations are affected, such as differential immigration and emigration or predation and competition by exotic species (Bierregaard et al. 1992; Andrén 1994; Barbosa and Marquet 2002; Hanski and Gaggiotti 2004).

Conservation strategies have strongly relied on the creation of nature reserves to minimize the disappearance of ecosystems, habitats, species, and populations, to maintain ecosystem structure and function, and to keep ecosystem services (Daily 1997; Margules and Pressey 2000; Ceballos et al. 2005). Unfortunately, fragmentation and isolation are problems affecting many nature reserves. A common outcome of isolation of reserves somehow correlated with their size and the impact of human activities and is the differential extinction of species and changes in population and community structure. Smaller reserves tend to lose larger and/or specialized species (Buchner 1987; Bierregaard and Lovejoy 1989; Klein 1989)**,** and fragmented populations many times shift from a continuous to a metapopulation structure (Hanski 1994; Lidicker and Koenig 1996; Ovaskainen et al. 2002; Ewers and Didham 2006). For conservation purposes, the evaluation of community structure and population dynamics in a particular reserve is fundamental to determining long-term management strategies (McCullough 1996; Wiegand et al. 2005). Local ecological interactions and species coexistence within small areas of "uniform habitat" are determined by population processes (Schluter and Ricklefs 1993). Competition and predation often tend to reduce diversity by eliminating taxa (local extinction), although predation can promote coexistence of increased number of prey species in some circumstances (e.g., Paine 1974; Witman 1987; Schröder and Richter 1999).

Temporal (i.e., seasonality) and spatial habitat heterogeneity have different effects on community and population processes, particularly on species richness and population dynamics and genetics (e.g., Hendrick et al. 1976; Levin 1976; Wiens 1976; Stenseth 1980; Brown and Harney 1993; Kelt 1995; Vázquez et al. 2000). These environmental factors are important determinants of the demography that affect population attributes, such as age structure, sex ratios, and reproductive rates (Bowers and Smith 1979; Van Horne 1982; Seagle 1985; Morris 1989; Fahrig 2003). In the temperate regions of central Mexico, seasonality is marked by profound shifts in the availability of resources related to climatic patterns (Soberón et al. 1991). Reproduction and

population dynamics of small mammals show a marked synchronicity with the time of bountiful resources at the end of summer (Sánchez-Cordero 1980; Canela 1981; Ceballos and Galindo 1984; Rojas 1984; Gómez 1990; Sánchez-Cordero and Canela 1991). This synchrony has been reported in species as different as Mexican vole (*Microtus mexicanus*), volcano mouse (*Neotomodon alstoni*), black-eared mouse (*Peromyscus melanotis*), deer mouse (*P. maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and volcano harvest mouse (*R. chrysopsis*) (Cervantes-Reza 1987; Gómez 1990; Sánchez-Cordero and Canela 1991).

In this study, we evaluate the community structure and population dynamics of small mammals in a 237-ha reserve in Mexico City. The reserve is completely isolated by urban neighborhoods and the composition of some plant and animal communities has been negatively affected by habitat fragmentation and isolation (Eguiate and Búrquez 1988; Parra et al. 1993, Chávez and Ceballos 1994). The effects of habitat loss in the species composition and populations dynamics of remaining small mammals are unknown. So, we specifically examine the following questions: (1) Are there historic changes in the species diversity and composition? (2) Are there introduced species? (3) Is there a differential use of microhabitat by native and introduced species of small mammals? and (4) What are the population dynamics of the native species in the reserve when compared to more extensive habitats?

MATERIALS AND METHODS

Study Area

The study area is in the 237-ha Pedregal Ecological Reserve (REPSA, by its acronym in Spanish), which is located at the main campus of the National University of Mexico, to the south of Mexico City, Distrito Federal, between 19°20'22" and 19°13'25" N and 99°08'26" and 99°14'03" W, at an elevation of 2540 m. (Figure 1). The climate is temperate sub-humid with a

Figure 1. The El Pedregal Ecological Reserve is located in southern Mexico city, completely surrounded by urbanized land.

summer rainy season lasting from May to October (García 1978). The average annual precipitation in the area is 870 mm. The reserve is covered by a thick layer of lava, produced from the eruption of Xitle volcano in 400 A.D. This produced an uneven topography including caves, ravines, and rocky promontories. As a result, there are a great variety of microenvironments.

Where the dominant vegetation association is xeric scrub, dominant life forms are herbs and shrubs. It is estimated that nearly 150 plant species have disappeared since the first survey was carried out in 1954 (Valiente-Banuet and De Luna 1990), and approximately 100 species characteristic of transformed habitats have appeared or have been introduced (Segura and Martinez-Ramos 1994). There are approximately 266 native species of plants (Rzedowski 1954; Valiente-Banuet and De Luna 1990). Some of the dominant shrub species taller than one meter are *Senecio praecox*, *Opuntia tormentosa*, *Agave ferox*, *Wigandia urens*, *Verbesina virgata*, *Buddleia cordata*, and *Buddleia parviflora*. The herbaceous layer is dominated by grasses, such as *Muhlenbergia robusta*, *M. rigida*, and *M. plicata*. Most plants are inactive from November to May (Rzedowski 1954). The vegetative period lasts from the end of May until August, while in September and October there are the maximum number of plants in fruit and flower. A few species of plants reproduce from November to January. In the mid 20th century, there were 37 species of mammals in the reserve, including 15 rodents (Villa 1953; Ceballos y Galindo 1984).

Trapping

Small mammals were sampled in two different protocols. First, the species diversity and composition were determined by 6-month sampling in 1989, 1990, and 2005 of the entire reserve using transects and grids of different lengths with Sherman traps. We did 11 sampling sessions using grids distributed at random in the reserve. The grids had 48 Sherman traps set in four lines with 12 traps each; lines were set 30 m aside, and traps were set 15 m apart. Traps were set during two nights.

In 2005, we sampled the southwest part of the reserve with five transects, 50 m apart, using 80 Sherman traps set each 10 m. Transects were changed to a different location every day for four consecutive days. Similarly, other places along the boundary of the reserve or outside the reserve were sampled occasionally using from five to 20 traps (Negrete 1991; Chávez and Ceballos 1994).

Second, to assess the population dynamics, we selected two 0.81-ha grids, separated by 50 m, placed in a relatively undisturbed scrub. Grids were set closely together to reduce environmental variance. In each grid, 100 traps were set at permanent sites in a 10 by 10 arrangement; traps were separated by a distance of 10 m. From September 1989 to October 1990, small mammals were trapped each month for three consecutive nights coinciding with the new moon. Traps were baited with a mixture of oats, peanut butter, and vanilla extract.

We recorded the following data from captured individuals: trap location, species, number of the individual (with ear tag), sex, reproductive condition (i.e., for females: state of the vagina--closed, opened, or plugged, state of mammary glands--not visible, enlarged, or lactating, and pregnancy--presence of embryos by palpation; for males: position of the testes--scrotal or abdominal), length of the foot, and weight (g). Animals were marked with numbered ear tags, except for *Reithrodontomys fulvescens* mice which, because of their size, were marked by toe clipping. All animals were released after being marked at the place of capture.

To estimate the abundance of insects in El Pedregal, we used a technique known as rug wall (Southwood 1988). This method utilized a 1 m^2 piece of rug with a 100 watt light bulb in one site separated 100-200 m from each plot. Sampling periods included three hours after sunset from January to October of 1990.

Microhabitat

In order to evaluate microhabitat use, we

measured habitat structure and plant species richness in April and May of 1990, taking each trap location as the center of a circle with a radius of 0.81 m for herbaceous plants and 5 m for trees and shrubs. Thirty-one variables reflecting habitat structure were measured (Appendix).

Analysis

To calculate species diversity, we used the Shannon-Wiener Index (H'), the maximum diversity (H max), and evenness (J') (Zar 1984). The diversity between grids was compared using Hutchenson t-test in Zar (1984). Densities were calculated by calculating the minimum number of live individuals that would explain the data (Krebs 1966). The density data were analyzed in a temporal and spatial manner. Loglinear models were used to model the number of individuals per month, grid, species, and sex. The loglinear analysis is an extension of the familiar chi-squared analysis of two-way contingency tables (tables of counts or responses) for which there are more than two variables. The objective was to study the relationships among the variables (James and McCulloch 1990). This produced a contingency table using a statistical package of general linear models (GLIM 1985).We used the non-parametric Mann-Whitney test (U) to compare differences in densities, because the data were not normally distributed.

To evaluate age structure in *Peromyscus,* we grouped organisms into three age classes: juveniles, subadults, and adults. These were defined by external morphological characteristics (e.g., type of pelage; Douglas 1969) and body mass. Juveniles have a homogenous gray pelage and a body mass of less than 14 g. Subadults have an ochre lateral line and a body mass between 14 and 18 g. Adults are an ochre-gray color with a weight greater than 18 g.

We used two indirect measures of survival: persistence and residence. Persistence was defined as the percentage of individuals surviving over time to exclude organisms captured only once and animals captured in the last month of trapping. Residence was considered as the average time in

which animals were present in the study area (Ceballos 1989).

To generate a reduced set of vegetation variables that accounted for most of the variability in the original microhabitat data, we used principal components analysis (PCA). This method utilizes orthogonal axes that are perpendicular and not correlated (Adler 1985). Each axis, therefore, does not duplicate the variance described by the previous axis. To determine a PCA for each grid, we used each trap location as an individual observation. Components with the highest eigenvalues, which are the components that best describe the variation by combining the most important variables, were used to describe microhabitat preferences of rodents. The preferences were identified in a horizontal manner. To see if there were associations with captures at each trap location, we used multiple regressions, where the number of captures was the dependent variable and the habitat variables derived by PCA were the independent variables (Adler 1985; Holbrook 1979).

RESULTS

Long-term changes in species diversity

We report temporal changes in species diversity and composition in three small mammal orders: Didelphiomorpha, Soricomorpha, and Rodentia (Table 1). There were 18 species of small mammals belonging to these orders in the reserve in the 1950s. Nine species from their families (Cricetidae, Geomyidae, and Sciuridae) have since then disappeared (Table 1; Figure 2). The Mexican ground squirrel (*Spermophilus mexicanus)*, Merriam´s pocket gopher (*Cratogeomys merriami)*, and Mexican vole (*Microtus mexicanus)* disappeared because of the loss of grasslands, which were restricted to small patches among the scrubland (Table 1).

The nine native species recorded in our study included the Virginia opossum (*Didelphis virginiana*), Chesnut-bellied shrew (*Sorex ventralis*), Mexican rock squirrel (*Spermophilus variegatus*), red-bellied

Table 1. Species of small mammals recorded in El Pedregal Ecological Reserve in 1953 (Villa 1953; Ceballos and Galindo 1984) and 1989-2007. The area covered by the lava flow was 40 km² in 1953 and 2.37 km² in 2007.

ORDER/Species	1953	This study	Extirpated	Vegetation type
DIDELPHIOMORPHIA	1	1	0	
Didelphis virginiana	+	+	0	All
SORICOMORPHA	2	1	1	
Sorex saussurei	+	+	0	Grasslands
Sorex ventralis	+	0	+	Grasslands
RODENTIA	15	7	9	
Spermophilus mexicanus	+	0	+	Grasslands
Spermophilus variegatus	+	+	0	Scrublands
Sciurus aureogaster	-	+	0	Woodlands
Cratogeomys merriami	+	0	+	Grasslands
Liomys irroratus	+	0	+	Scrublands
Microtus mexicanus	+	0	+	Grasslands
Baiomys taylori	+	+	0	Grasslands
Neotoma mexicana	+	+	0	Scrublands
Peromyscus difficilis	+	+	0	Scrublands
Peromyscus gratus	+	+	0	Scrublands
Peromyscus levipes	+	0	+	Scrublands
Peromyscus maniculatus	+	0	+	Grasslands
Peromyscus melanotis	+	0	+	Grasslands
Reithrodontomys	+	+	0	Grasslands
Reithrodontomys megalotis	+	0	+	Grasslands
Sigmodon hispidus	+	0	+	Grasslands

squirrel (*Sciurus aureogaster*), Northern pygmy mouse (*Baiomys taylori*), Mexican woodrat (*Neotoma mexicana*), Southern rock deermouse (*Peromyscus difficilis*), Saxicoline deermouse (*Peromyscus gratus*), and Fulvous harvest mouse (*Reithrodontomys fulvescens*). The red-bellied squirrel was observed but not captured. Additionally, two species of introduced rodents, the roof rat (*Rattus rattus*) and the house mouse (*Mus musculus*), were recorded in perturbed habitats. Locally extinct species disappeared because of habitat loss and other reasons.

In our study, all native species, with exception of the opossum, rock squirrel, Southern rock deermouse, and Saxicoline deermouse, were exclusively recorded in the continuous native scrub of the reserve.

Therefore, they are good indicators of the sites in the reserve that maintain the less perturbed habitats. Interestingly, no introduced rodents (i.e., roof rat and house mouse) were found in the continuous scrub of the reserve. These species were found in the most perturbed sites, such as road medians and garbage treatment areas, outside the reserve or along its boundary.

Grid species diversity and abundance

We recorded only six species in 4200 trap-nights for each of the two grids. Altogether, 352 individuals were captured-recaptured 1941 times. In general, trapping success was approximately 23%, with minor differences between grids. Species recorded were Virginia opossum, Chesnut-bellied
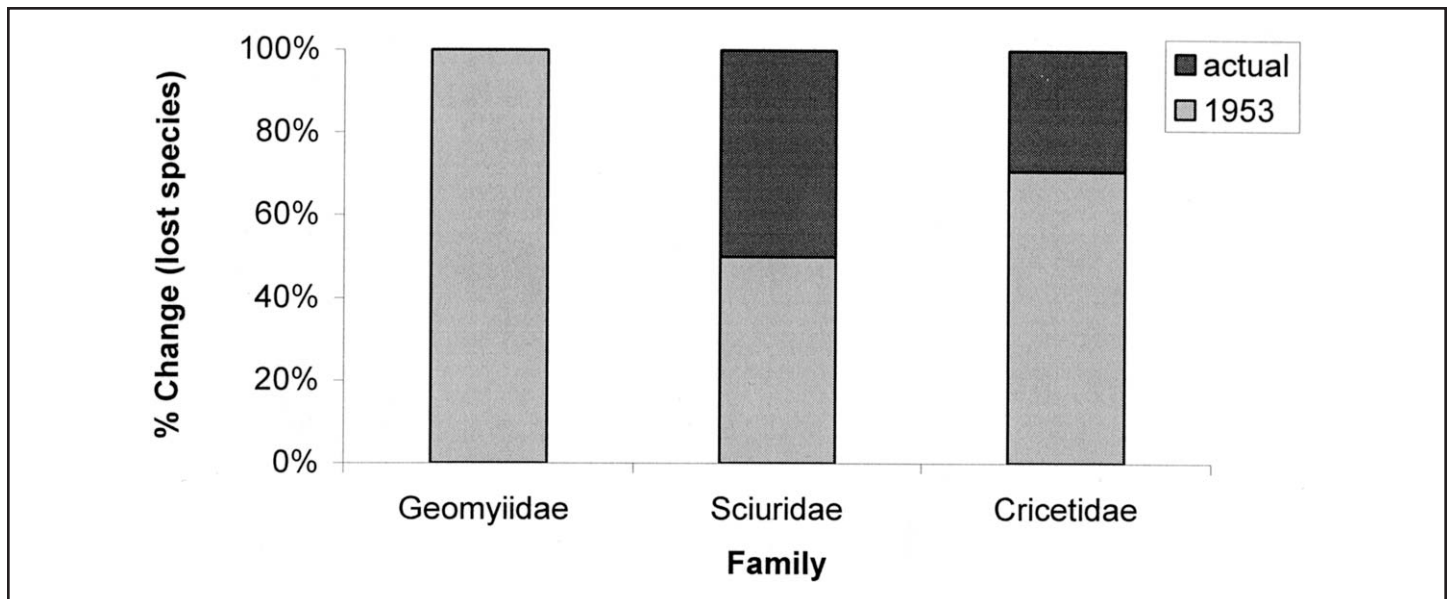
Figure 2. Percentage changes in the number of species in various families at El Pedregal Ecological Reserve.

shrew, a rock squirrel, Mexican woodrat, Saxicoline deermouse, and Fulvous harvest mouse. All species are mentioned by their scientific generic name hereafter.

There was greater diversity and evenness of all species and for cricetid rodents when grid 1 was compared to grid 2 (Table 2). When whole species were analyzed, diversity values were significantly different (t = 3.43; p < 0.001). Some significant differences were also found for cricetid rodents (t = 4.06; p < 0.001). Comparing the total number of species captured per season, it is evident that the 1990 rainy season (H' = 0.86) reveals greater diversity than the 1989 post-rainy season (H' = 0.64; t = 1.68; p < 0.01) and the 1990 pre-rainy season (H' = 0.57; t = 2.15; p < 0.01), owing to a greater number of individuals of the shrew (*Sorex saussurei*), marsupial (*Didelphis virginiana*), and ground-squirrel (*Spermophilus variegatus*).

For cricetid rodents there is a greater diversity in the 1990 pre-rainy season (H' = 0.40) than in the 1989 post-rainy season (H' = 0.64; t = 2.88 p < 0.001) owing to the greater number of individuals of *Neotoma* and *Reithrodontomys* captured and to the decrease in captures of *Peromyscus* (Table 2). The diversity of cricetid rodents in nearly all of the seasons was larger in grid 1 than in grid 2 (Table 2), owing to

an increase in the abundance of *Neotoma* and *Reithrodontomys*. In grid 1, the greatest diversity occurred in the post-rainy season (pre- vs. post-rains; H' = 050 *vs.* 0.84; t = 3.03; p < 0.001) owing to an increase in the abundance of *Neotoma* and *Reithrodontomys* and a decrease in *Peromyscus*, while diversity was not significantly different between seasons in grid 2.

Species were classified as abundant (represented by > 30 individuals), common (10 to 29 individuals), or scarce (< 9 individuals). Two species (*Peromyscus* and *Neotoma*) were abundant, one (*Reithrodontomys*) was common, and three (*Sorex*, *Spermophilus*, and *Didelphis*) were scarce (6, 5, and 8 individuals respectively; Table 3).

Population dynamics

The average monthly population density for all species was 36.28 ± 22.4 individuals/ha. Population density showed a continuous increase from September until December, when it peaked at 57.5 individuals/ha. After December, there was a decline until it reached a minimum of 22.8 individuals/ha between July and September. The growth in density occurred after the period of rains (Figure 3). Density differed significantly between grids ($U = 82$, $P < 0.05$). Population changes in *Peromyscus* and *Neotoma* followed a similar tendency, with a marked

increment following the rainy season, but there were significant differences between the grids in both *Peromyscus* ($U = 63.5$, $P < 0.05$) and *Neotoma* (Figure 3).

Interaction between variables

One of the advantages of the log-linear model is the possibility of making multiple comparisons among variables. For that, we employed the total number of individuals of each of the three species found in both grids (*Peromyscus*, *Neotoma*, and *Reithrodontomys*) as the dependent variable and the distribution of this value of abundance with respect to species, sex, site, month, and grid as factors to analyze. We found that the population trends were different for *Peromyscus*, *Neotoma,* and *Reithrodontomys* and that there was a lower number of individuals overall for the last two than for the former ($L^2 = 3.69$ and $L^2 = 68.07$, $P < 0.01$).

When all species of cricetid rodents are pooled, it is seen that there were less individuals in October than in December of 1989 ($L^2 = -2.02$, $P < 0.05$): (1) the greatest abundance was from June to September 1990; (2) more individuals were captured in November than from May to October 1990 ($L^2 = 2.67$ to 4.53, p < 0.01); and (3) the peak in December was significantly different from that from March to October 1990 ($L^2 = 2.18$ to 4.84, p < 0.01).

Table 2. Data of seasonality responses of the small mammals species at El Pedregal, D.F. Mexico.

Species	Grid 1 – Season				Grid 2 – Season				Total – Season			
	Pre-Rainy	Post-Rainy	Rainy	Total	Pre-Rainy	Post-Rainy	Rainy	Total	Pre-Rainy	Post-Rainy	Rainy	Total
Peromyscus gratus	76.00	47.00	33.00	129.00	86.00	70.00	40.00	149.00	162.00	117.00	73.00	275.00
Neotoma mexicana	12.00	19.00	6.00	29.00	8.00	10.00	1.00	19.00	20.00	29.00	7.00	48.00
Reithrodontomys fulvescens	2.00	6.00	3.00	14.00	0.00	0.00	1.00	1.00	2.00	6.00	4.00	12.00
Didelphis virginiana	0.00	0.00	6.00	6.00	0.00	0.00	2.00	2.00	0.00	0.00	8.00	8.00
Sorex sp.	3.00	0.00	1.00	4.00	1.00	0.00	1.00	2.00	4.00	0.00	2.00	6.00
Spermophilus variegatus	1.00	0.00	0.00	1.00	2.00	0.00	1.00	3.00	3.00	0.00	1.00	4.00
Number total of inviduals	94.00	72.00	49.00	183.00	97.00	80.00	46.00	176.00	191.00	152.00	95.00	353.00
Number of Cricetid individuals	90.00	72.00	42.00	172.00	94.00	80.00	42.00	169.00	184.00	152.00	84.00	335.00
H' total	0.67	0.84	1.03	0.98	0.44	0.38	0.59	0.58	0.57	0.64	0.86	0.81
H' Cricetid	0.50	0.84	0.66	0.72	0.29	0.38	0.33	0.39	0.40	0.64	0.47	0.58
Hmax total	1.61	1.10	1.61	1.79	1.39	0.69	1.79	1.79	1.61	1.10	1.79	1.79
Hmax Cricetid	1.10	1.10	1.10	1.10	0.69	0.69	1.10	1.10	1.10	1.10	1.10	1.10
J' total	0.42	0.76	0.64	0.55	0.32	0.54	0.22	0.33	0.35	0.63	0.48	0.45
J' Cricetid	0.45	0.76	0.60	0.66	0.42	0.54	0.42	0.35	0.32	0.63	0.43	0.60

Fewer individuals were captured in June and July 1990 than from October 1989 to April 1990 ($L^2 = 2.20$ to 4.84, $p < 0.01$), while fewer were captured in August and September 1990 than from October 1989 to May 1990 ($L^2 = 2.85$ to 4.53, $p < 0.01$). November 1989 to February 1990 had more individuals than October 1990 ($L^2 = 2.58$ to 3.36, $p < 0.01$).

More *Reithrodontomys* males were captured than females, but the ratio was essentially 1:1 for all other species. *Neotoma* was significantly more abundant in February, March, and April 1990 than in October and November 1989 or October 1990 ($L^2 = 2.11$ to 2.87; $p < 0.01$).

When the abundance of all species was analyzed, the only significant difference between grids was in the case of *Reithrodontomys*, which was significantly more abundant in grid 1 ($L^2 = 3.61$, $p < 0.001$). With all species analyzed separately, *Peromyscus* had significantly more individuals in grid 2 ($L^2 = 3.86$ $p < 0.0001$) as well as more males than females ($L^2 = 4.89$ $p < 0.0001$). Fewer individuals were found in September 1989 than in October, November, and December 1989 or in January and February 1990 ($L^2 = 2.03$ to 3.95; $p < 0.01$) and more individuals were found between October and April 1989 than from June to October of the same year ($L^2 = 1.98$ to 3.09; $p < 0.01$). The peak month (December) had a greater abundance than October 1989 or the months from March to October 1990 ($L^2 = 2.18$ to 4.21; $p < 0.01$).

There were significantly more *Neotoma* females in grid 1 ($L^2 = 2.85$ $p < 0.0046$) and more individuals overall in the peak months (February to April) than in September, October, and November 1989 or October 1990 ($L^2 = 1.99$ to 2.96; $p < 0.01$), and more individuals in March than in June.

Biomass and body weight

The average monthly biomass of rodents in the two grids was 1083 g/ha. The biomass followed the same annual trend as population densities with similar biomass in each grid. We found the lowest biomass

Table 3. Comparison of the diversity for seasons between each of the grids, for all cricetids and for all species.

Cricetid species				All species			
	Grid 2				Grid 2		
Grid 1	Post-rainy	Pre-rainy	Rainy	Grid 1	Post-rainy	Pre-rainy	Rainy
Post-rainy	4.44 ***	5.39 ***	4.30 ***	Post-rainy	4.44 ***	3.31 ***	n.s.
Pre-rainy	n.s.	1.89 ***	1.83 *	Pre-rainy	2.34 ***	1.67 **	n.s.
Rainy	2.56 **	1.94 *	2.48 **	Rainy	4.24 ***	3.57 ***	n.s.

Significance: * = p<0.05; ** = p<0.01; *** = p<0.001

in September 1989 (741 g/ha) and the highest biomass in February 1990 (2365.8 g/ha). The biomass of *Peromyscus* in grid 2 contributed 71.2% of the total, and that was significantly different from biomass in grid 1 ($t = 2.13$, $df = 26$, $P < 0.05$). *Peromyscus* contributed 60.9% of the total in both grids (Figure 4). In *Neotoma*, the biomass was similar in both grids, but grid 2 showed a higher biomass of females than males ($X^2 = 2.59$, $df = 26$, $P < 0.025$). Body mass of adult *Peromyscus* was similar between males and females (22 ± 2.37 g and 22.48 ± 3.17 g respective), while that of *Neotoma* was 173 ± 34 g for males and 160.67 ± 21.6 g for females.

Reproduction and age structure

In both *Peromyscus* and *Neotoma,* we found no evidence of reproduction in males or females in January (Figure 5). In *Peromyscus*, the peak of reproduction was at the end of the rainy season (September and October) during 1989. However, in 1990 there was a marked drop in the number of individuals, and that year the proportion of reproductive individuals peaked in July (with 63% of females and 52% of males). The proportion of individuals in reproductive condition then declined until September.

The age structure of *Peromyscus* varied drastically in the study (Figure 6a). The largest number were juveniles found in September and October, the greatest number were subadults found in February, and the major number of adults were trapped in June (44). The smallest number of adults was located in October (24).

Recruitment

The recruitment of all species dropped from September 1989 until January 1990 and then rose from February to June (Figure 6b). It then fell in July (12%), growing considerably in October (57%). For *Peromyscus*, it dropped from September 1989 to March 1990 (100%), then grew slightly in April with 14 individuals (19%). July 1990 was the month with the lowest recruitment (four individuals or 14%); it then grew considerably from July until October (with 20 individuals (55%)), when almost half the organisms were new. The patterns of recruitment in *Neotoma* were irregular. Twice, when only two individuals were captured and both were new, it stretched to 100%.

Survival

The persistence of *Peromyscus* and *Neotoma* was similar in the first months of the study; however, six (3.1%) *Peromyscus* individuals were present after 13 months of trapping. Fifty percent disappeared in three months and the residence was 3.6 months. Only one (4%) individual of *Neotoma* persisted nine months, with 52% disappearing in three months. The time of residency was 2.12 months with females lasting 1.64 months and males lasting 3.85 months.

Spatial use of habitat

The PCA shown in four principal components had eigenvalues greater than one and they explained 68% of the microhabitat variation. The maximum height, diameter at breast height (dbh), and percentage cover were the three variables that contributed to a high proportion of variation in principal component 1 (21% of variation), which represented the biomass of trees.

The number of trees was an important factor in principal component 2 (18.49%), which explained the diversity and density of trees. The height of the grasses and herbs (number of stems and maximum height) was a factor contributing to principal component 3 (15.63%). Finally, the maximum height of herbs and species of bushes represented principal component 4 (12.6%).

Analyses microhabitat variables among grids showed that there were not significant differences (U = 986 p = 0.90). Captures of *Peromyscus* and *Neotoma* were not correlated with the variables derived from the principal components in the two grids. The relationship between the rodents and the microhabitat variables was not clear. All of the traps captured *Peromyscus* at least once, and they showed a wide utilization of microhabitat. *Neotoma* showed a similar tendency, even though there were traps without a capture.
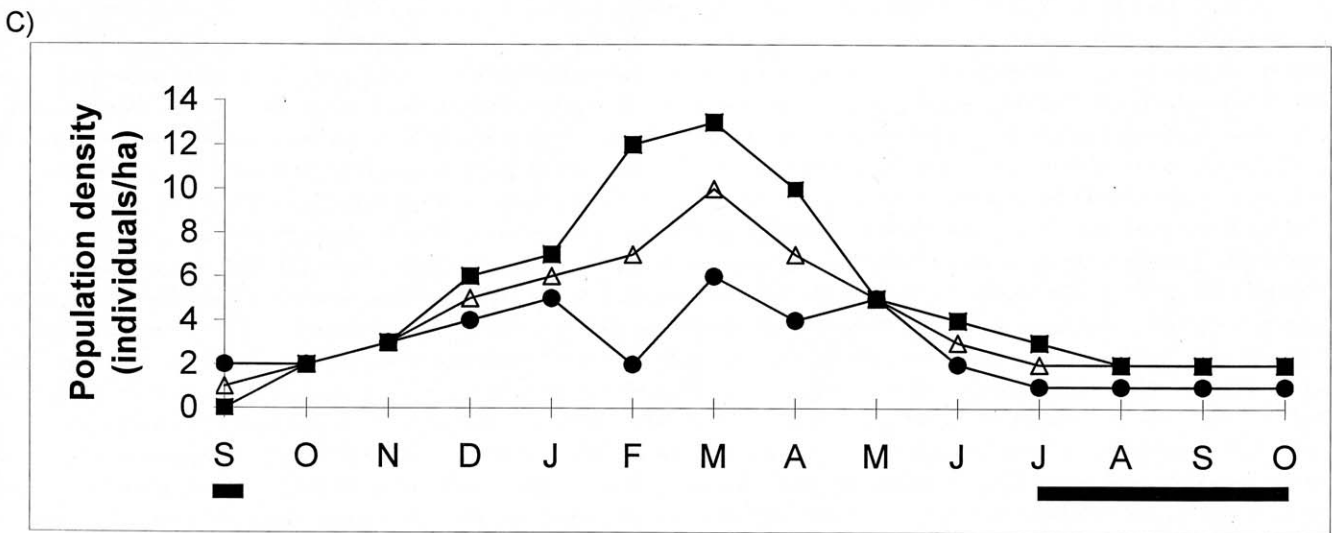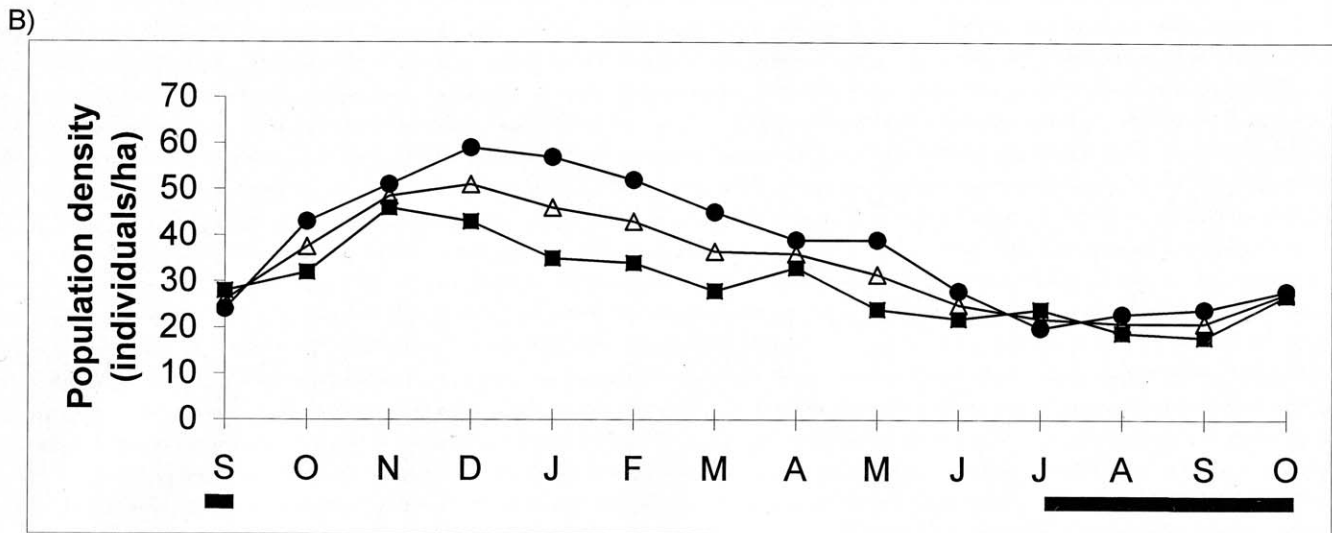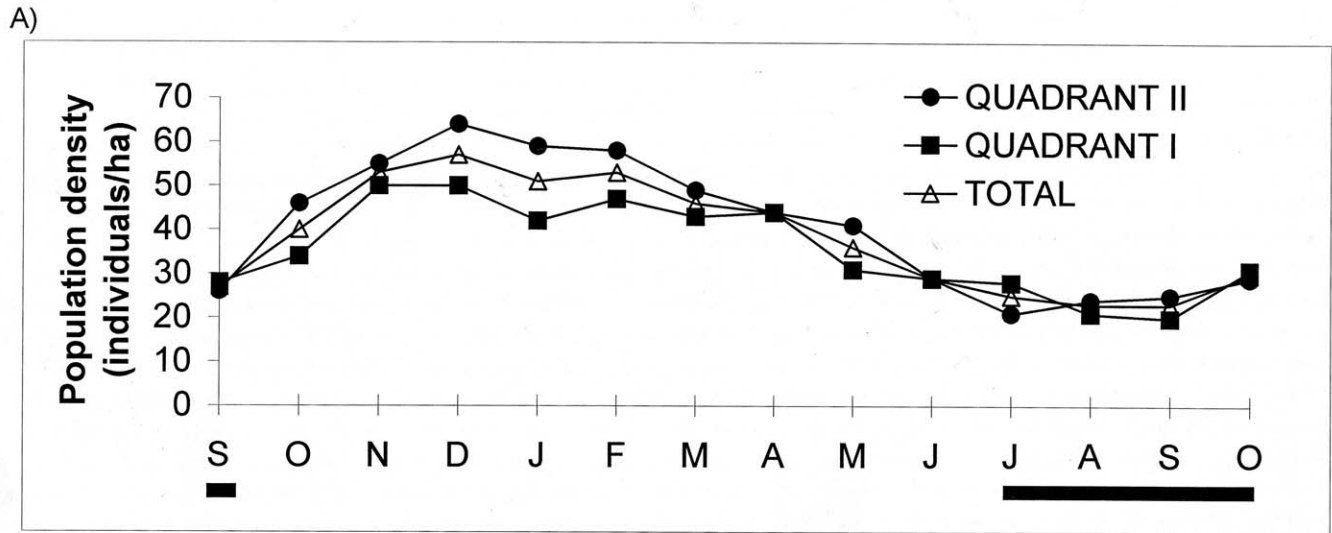
Figure 3. Population density over time of all species combined (A), *Peromyscus gratus* (B) and *Neotoma mexicana* (C) at El Pedregal Ecological Reserve. The line under the months represents the season of rains in all the graphs.
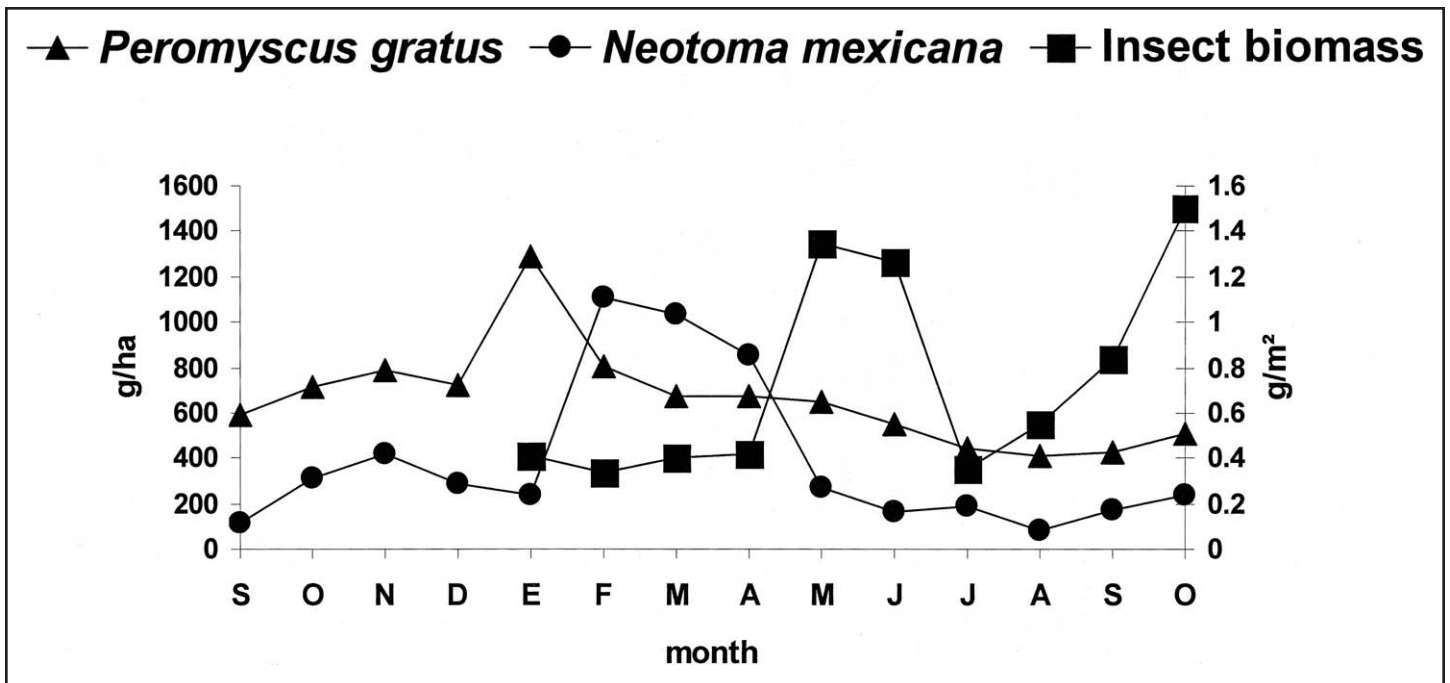
Figure 4. Biomass trends over time of *Peromyscus gratus* (triangle) and *Neotoma mexicana* (circle) at El Pedregal Ecological Reserve.
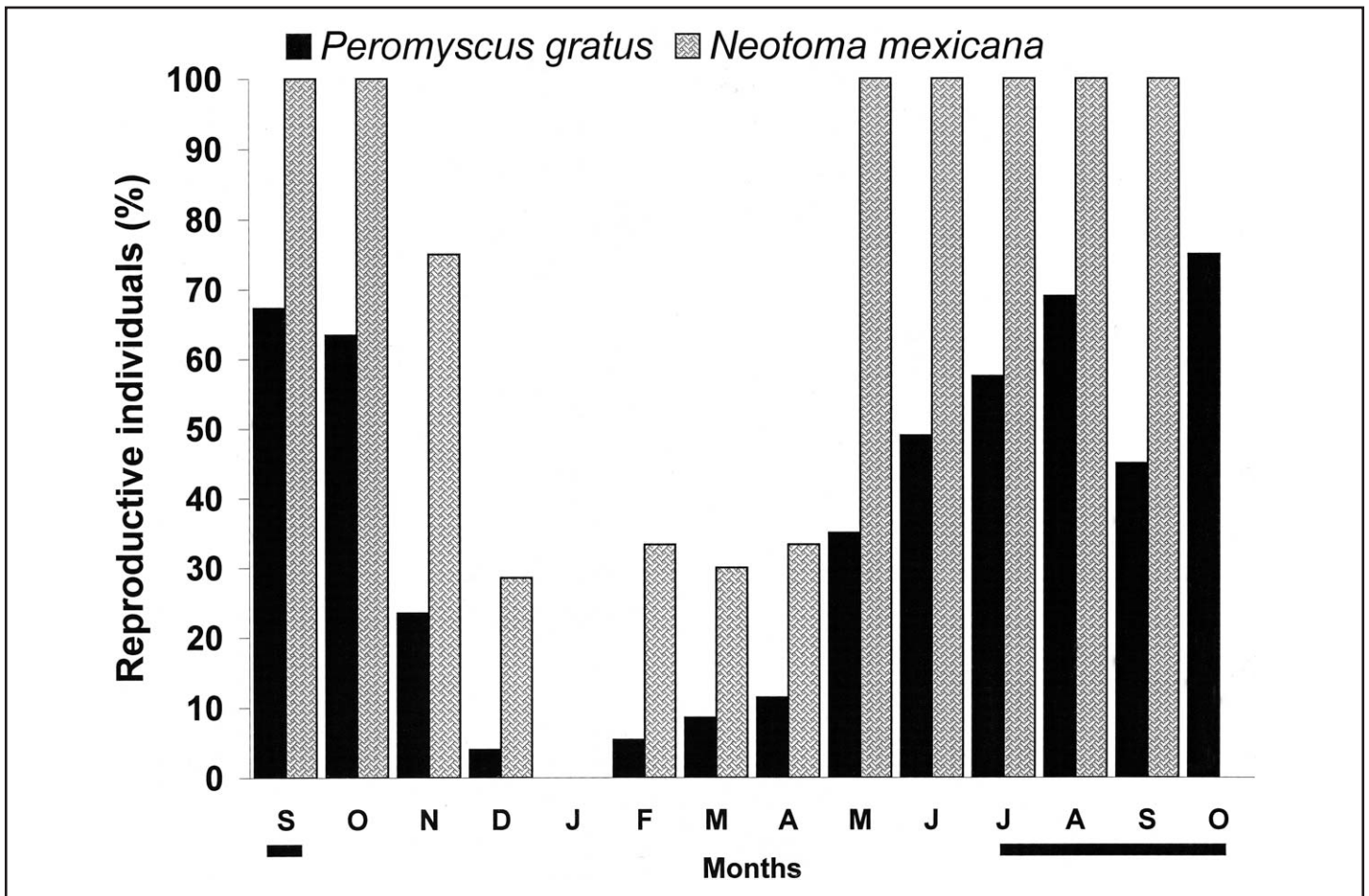

Figure 5. Percentage of reproductive individuals of *Peromyscus gratus* (shared bar) and *Neotoma mexicana* (unshared bar) at El Pedregal Ecological Reserve.
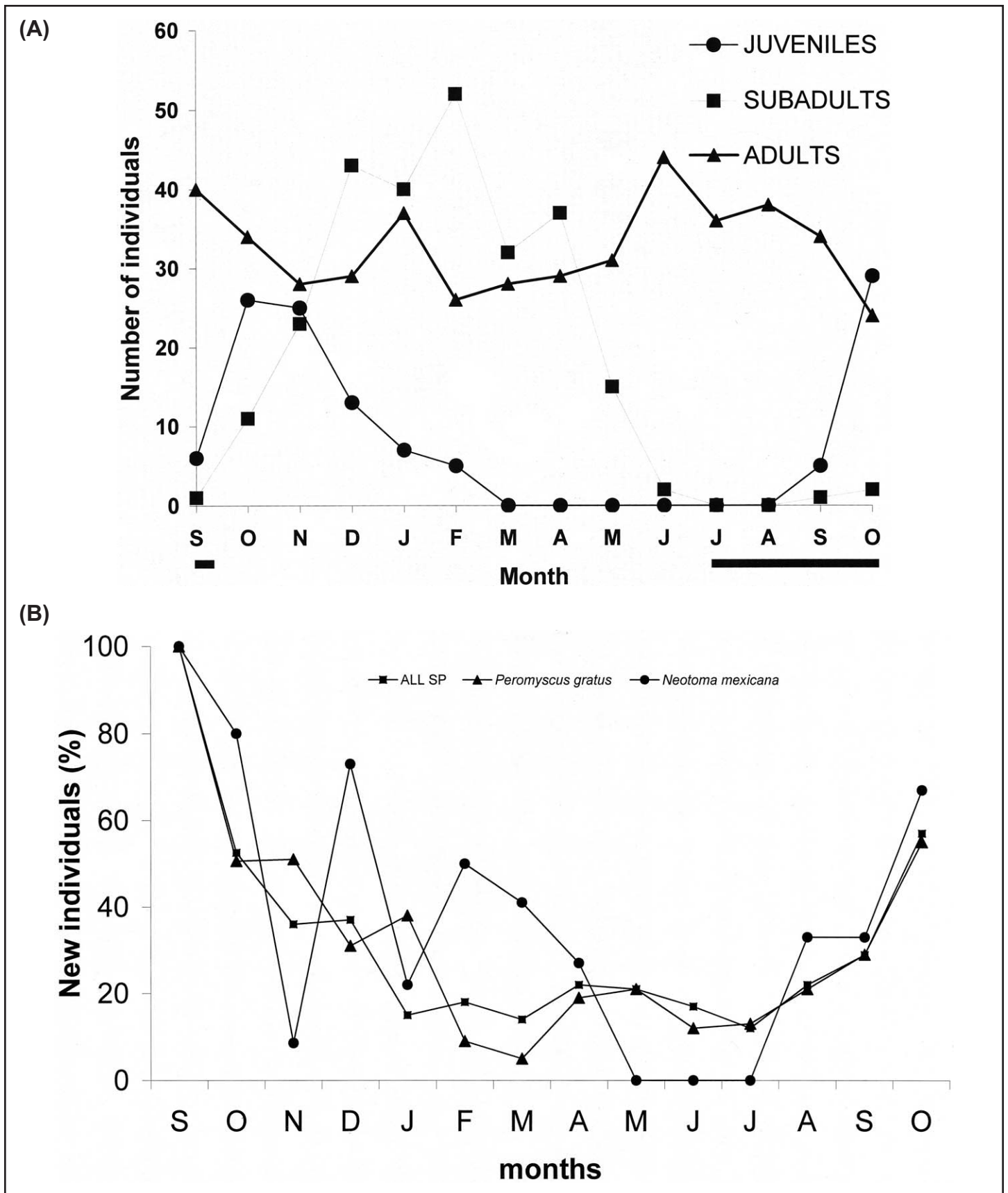
Figure 6. (A) Changes in age structure over time in populations of *Peromyscus gratus* and (B) recruitment of all species (square), *Peromyscus gratus* (triangle) and *Neotoma mexicana* (circle) at El Pedregal Ecological Reserve.

DISCUSSION

Long-term changes of species diversity

In El Pedregal and its surroundings areas, about 60% of the species historically reported for the zone have disappeared because of the disappearance of suitable habitats, such as grasslands (Villa 1953; Ceballos and Galindo 1984; Negrete 1991; Chávez and Ceballos 1992, 1994). The 90% area reduction of El Pedregal de San Angel from 40 to less than 3 km^2 caused the destruction of several habitats and microhabitats, such as grasslands, shrub lands, and oak (*Quercus* spp.*)* and pine (*Pinus* spp.) forests (Alvarez et al., 1982). The species that survived were the ones that could either tolerate the changes or their habitat was the scrubland that still persists in the reserve. El Pedregal has remained isolated from other natural areas, and that has impeded the flow of species. As a result, there has been a notable reduction of species richness in plants as well as animals. However, the reserve has an important role in the surviving mammal species and many other vertebrate, invertebrates, and plants, including three endemic species found nowhere else on Earth (Valiente-Banuet and De Luna 1990; Sóberon et al 1991; Castillo et al 2004).

Habitat by native and introduced species of small mammals

The scrubland of the reserve where native species survive lacks introduced rodents, indicating the exclusion of the introduced species by the native ones. Although at this point it is difficult to define the exclusion mechanisms, it is likely they are related to competition and food availability. Medium and large size introduced mammals, such as cats (*Felix catus*) and dogs (*Canis lupus familiaris)*, are common inside the reserve and have diseases such as rabies and toxoplasmosis (Suzán and Ceballos 2005). The presence of feral mammals and the small size and isolation of the reserve threaten the long term survival of the native species, such as rodents and carnivores (Chávez and Ceballos 1992, 1994; Suzán and Ceballos 2005). Good management practices, such as eradication of feral dogs and cats, are required to ensure the native species.

Population dynamics

The rodent community of the El Pedregal thickets has a relatively low species richness and diversity when compared to both temperate and tropical communities (Brown 1967; Fleming 1971, 1973, 1974; Miller and Getz 1977; Southern 1979; Sánchez-Cordero 1980; Anthony et al. 1981; Baca del Moral 1982; Brown 1984; Rojas 1984; Ceballos 1989; Rabinowitz and Nottingham 1989; Goméz 1990; Medellín 1992; Mares and Ernest 1995). The low number of species in El Pedregal is related to historic changes associated with human perturbations that have reduced and fragmented the habitat and modified the structure and composition of the vegetation.

Population dynamics and reproduction were linked to the availability of food, such as the period from September until December when there was a maximum number of plants in fruit and flower (Rzedowski 1954). This relationship has been documented in temperate climates (Delany 1974; Solomon 1977; Southern 1979; Stoddart 1979; Lomnicki 1987; Vázquez et al. 2000). When a synchrony exists between food production and reproduction, it results in well defined annual population growth (e.g., Prieto 1988; Ceballos 1989, 1990; Goméz 1990; Sánchez-Cordero and Canela 1991).

Population densities fluctuated among species, but the densities of all species increased toward the end of the rainy season, which coincided with the production of seeds and fruits (Rzedowski 1954), whereas the biomass and density of insects increased at the beginning of the rainy season, with a peak at the end of September and in October (Cano-Santana 1987; Chávez 1993; Rios 1993).

These patterns are very similar to those observed in the temperate zones south of Mexico City where the maximum population also coincides with the rainy season between October and December (Sánchez-Cordero 1980; Goméz 1990).

The population changes in our sample sites were generally very similar, but significant differences exist in the densities between the two grids, which were separated by 50 m. This seems to indicate that there are microhabitat differences in productivity and availability of resources between the grids.

The increase in *Peromyscus* densities from September to December is related to the reproductive events, which agrees with information found for a similar species in the south of Mexico City (ex., *P. melanotis) (*Goméz 1990). Although for other species, such as *P. maniculatus*, the population growth occurs between November and March (Sánchez-Cordero 1980; Sánchez-Cordero and Canela 1991) and in spring and fall (Rojas 1984). In other temperate zones, the high densities of *P. maniculatus* occur in summer (M'Closkey 1972; Merrit and Merrit 1980; Millar 1984, 1989).

The reproductive patterns of *P. gratus* showed that the largest proportion of females and males were found in a reproductive condition during the rainy season (June to September). This is similar to findings for *P. truei* in Mesa Verde National Park, Colorado, USA, where the period of major availability of resources occurs between April and September, caused by the thaws at the beginning of April and by the effect of the summer rains in the Rocky Mountains where the reproductive principal of activity occurred from April to September and declined gradually until October (Douglas 1969).

The reproductive period is probably influenced strongly by climatic changes that directly affect vegetation growth and indirectly affect other populations, such as insects. A reduction of water and food has generally been associated with population declines, and if there is a supplemental supply of resources, it will increase reproduction (Bradford 1974, 1975).

The most relevant aspect of this study was the documentation of marked variability in the observed population and community parameters. This variation is the result of the high microhabitat heterogeneity and low environmental complexity in El

Pedregal. The rodents in El Pedregal live in a complex mosaic of microhabitats that profoundly influence the cycle of life and community structure, which results in some variation of spatial and temporal scales.

It has been suggested that the vegetation cover plays a very important role in the population dynamics and community structure, causing different responses from the species in spatial and temporal scales (Rosenzweig and Winaker 1969; Holbrook 1978, 1979; Price 1978; Kitchings and Levy 1981; Adler 1985). In El Pedregal, there is probably heterogeneity at the microhabitat scale that does not determine, in a marked form, the presence or distribution of species. The importance to the rodent community probably lies at the macro level or is owed to the profound effect of the fragmentation and reduction of habitat in El Pedregal, which in a relatively short time separated entire communities.

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Appendix. Designation, descriptions, and sampling methods for thirty-one variables measured in palo loco (*Senecio praecox*) thickets.

Variable	Methods
1) slope	
2) number of herb species	the number of herb species in a circle of 0.8 m radius
3) number of herbs	the number of individual herbs in the same circle as (2)
4) herb cover	herb cover in the same circle as (2), calculated with the hyperbolic formula $((D1+D2)^2/4)*p$
5) median height of herbs	median height of herbs in the same circle as (2)
6) maximum height of herbs	maximum height of herbs in the same circle as (2)
7) minimum height of herbs	minimum height of herbs in the same circle as (2)
8) number of herb stems	the number of herb stems in the same circle as (2)
9) grass cover	same as (4) for the grass cover
10) grass area	the sum of basal areas of grass bunches in the same circle as (2)
11) median height of grass	the median height of grass bunches (without reproductive structure) in the same circle as (2)
12) number of bush species	the number of bush species in a circle of 5 m radius
13) number of bushes	the number of individual bushes larger than 0.10 m in a circle of 5 m radius
14) number of bush stems	the number of bush stems in the same circle as (13)
15) bush cover	bush cover in the same circle as (13), calculated with the hyperbolic formula $((D1+D2)^2/4)*p$
16) median height of bushes	median height of bushes in the same circle as (13)
17) maximum height of bushes	maximum height of bushes in the same circle as (13)
18) minimum height of bushes	minimum height of bushes in the same circle as (13)
19) number of woody species	number of tree species with dbh > 0.05 m in the same circle as (13)
20) number of woody individuals	number of individual trees with dbh > 0.05 m in the same circle as (13)
21) number of tree stems	the number of tree branching down to 0.3 m
22) woody cover	same as (15) for the woody cover
23) median height of trees	same as (16) for the woody cover
24) maximum height of trees	same as (17) for the woody cover
25) minimum height of trees	same as (18) for the woody cover
26) dbh	the sum of dbh values of all trees in the same circle as (13) (The dbh is the tree trunk diameter at breast height (1.5 m) .)
27) litter depth	measurement of litter depth in cm, taken in four directions (NE, NW, SW, SE)
28) number of vine species	the number of vine species in the same circle as (13)
29) density of woody stems	the woody stems number to touch one rod (0.8 m of largest) to take how center the tramp station.
30) number of grass bunch species	the number of grass bunch species in the same circle as (13)
31) number of grass bunches	the number of grass bunches in the same circle as (13)