Spatial and temporal organisation of small mammal communities in the Monte desert, Argentina

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ABSTRACT

The coexistence of desert small mammals can be explained by differences in microhabitat use, morphology, body size, diet and foraging. The aim of this study was to quantify the structure of small mammal assemblages and the seasonal fluctuations in their abundance using mark – recapture techniques in habitats of different structural heterogeneity (mesquite forest, creosotebush community, and sand dunes) in the temperate Monte desert of Argentina. Habitat heterogeneity was characterised by 10 vegetation variables. The mesquite forest and the creosotebush community showed the highest diversity and habitat heterogeneity. The relative abundance of each species underwent remarkable variations between habitats. The sigmodontinae rodents *Graomys griseoflavus* and *Eligmodontia typus* were the dominant species in the mesquite forest and sand dunes, respectively, whereas no dominant species was observed in the creosotebush habitat. Abundance varied throughout the year, reaching maximum density in autumn and spring.

KEY WORDS
desert small mammals,
diversity,
habitat use,
Monte Desert.

RÉSUMÉ

La coexistence des petits mammifères du désert peut être expliquée par la partition des ressources telles que l'utilisation du microhabitat, la morphologie, la taille corporelle, la diète et la recherche des aliments.

Le but de cette étude était présenter la structure de la communauté de petits mammifères dans des habitats avec différentes complexités structurelles ("mesquite forest", "creosotebush community" et les dunes) dans le désert tempéré du Monte d'Argentine, ainsi que les fluctuations saisonnières dans son abondance. Des techniques de capture et re-capture ont été utilisées.

L'hétérogénéité de l'habitat était caractérisée par dix variables. La forêt du "mesquite" et la communauté de "creosotebush" ont montré la plus grande diversité et complexité de l'habitat. L'abondance relative de chaque espèce a souffert des variations importantes parmi des habitats.

Graomys griseoflavus et *Eligmodontia typus* (Rodentia, Sigmodontinae) étaient les espèces dominantes dans la forêt du « mesquite » et les dunes respectivement. L'abondance a souffert des variations annuelles arrivant aux densités maximales à l'automne et au printemps.

MOTS CLÉS
petits mammifères désertiques,
diversité,
perte d'habitat,
Monte Desert

INTRODUCTION

The deserts of the world are characterised by extreme heterogeneity in climate, soil and history (Noy-Meir 1979/1980); these have marked effects on the ecosystem, particularly on total energy, water, nutrient flow and species survival (Noy-Meir 1974). Many studies on desert small mammals reveal that each species responds differently to biotic and abiotic features of the environment. Thus, only a small proportion of local habitat patches can provide suitable conditions for survival and reproduction (Brown & Kurzius 1987). The "complexity" and "heterogeneity" of the habitat (i.e. vertical and horizontal variation respectively) were hypothesized to increase species diversity, as they are make up of different microhabitats that can be occupied by species with different requirements (Rosenzweig & Winakur 1969; Holbrook 1978, August 1983, Price 1986). Resource partitioning appears to be a widespread mechanism for coexistence of desert rodents. Microhabitat use, competition, morphology, body size, diet and foraging behaviour of these rodents facilitate their coexistence (Kotler 1989, Scott & Dunstone 2000).

In the Central Monte Desert (Argentina) there are habitat patches with different degrees of vegetation cover (i.e., open areas, shrub steppe, sand dunes, and open woodlands, Morello 1958). On these sites it is possible to find a set of up to five coexisting species of small mammals (less than 100 g) that differ in morphology, body size, diet, and habitat preferences (Ojeda 1989). All of these species are nocturnal and omnivorous, but show trends toward insectivory, folivory or granivory (Campos *et al.* 2001). The silky mouse *Eligmodontia typus* F. Cuvier, 1837 is a small rodent with elongated hind limbs allowing the species to hop at times and escape from predators, especially in open areas (Mares 1975, 1983; Vásquez 1994). The vesper mouse *Calomys musculinus* (Thomas, 1913) with similar body size but lacking these morphological characteristics, is found in habitats with high grass cover (Gonnet & Ojeda 1998), where the larger grass mouse *Akodon molinae* Contreras 1968, is found in habitats with dense vegetation (Corbalán & Ojeda 2001). Another common rodent species is the "pericote" *Graomys griseoflavus* (Waterhouse, 1837), inhabiting a wide variety of habitats (Redford & Eisenberg 1992). This is the largest species of the assemblage, and is able to use trees for foraging and nesting due to its climbing abilities (Mares 1977). The common desert opossum *Thylamys pusillus* (Desmarest, 1804) is a small insectivorous marsupial that coexists with these rodents and can be found in very dry areas, in thorn scrub, or along watercourses with dense vegetation (Redford & Eisenberg 1992). It is capable of conserving water and can use high nitrogen sources that normally entail greater excretory water loss to overcome periods of food shortage (Diaz *et al.* 2001).

In this paper we report on the spatial and temporal species composition and abundance of small mammal assemblages in habitats with different structural heterogeneity in the temperate Monte Desert of Argentina. Our working hypotheses were that: a) more heterogeneous habitats would have higher diversity of small mammals, and b) habitats with different heterogeneity will be dominated by different small mammal species according to their ecomorphological attributes (Mares 1975, 1977; Ojeda 1989).

MATERIALS AND METHODS

STUDY SITE

The study was conducted in the Ñacuñán Biosphere Reserve (12,800 ha), 200 km southeast of Mendoza, Argentina (34°02'S, 67°58'W) (Ojeda *et al.* 1998). Biogeographically, the area belongs to the Monte biome (Cabrera & Willink 1980). The climate in the reserve is semi-arid and seasonal, with hot humid summers and cold dry winters. Mean annual precipitation is 330 mm and average maximum and minimum temperatures (1972-1990) range from 32.4°C and 16°C in January to 14.9°C and – 0.9°C in July, respectively (Guevara *et al.* 1996).

The vegetation in the area is xerophytic, and several plant communities can be distinguished (Roig 1971; Roig & Rossi 2001). We selected three major habitat types for this study:

1) *Mesquite forest*: This is the most representative community in the Reserve due to its size and number of strata. The tree stratum in this habitat is dominated by open woodlands of *Prosopis flexuosa* (Fam. Leguminosae), associated with isolated specimens of *Geoffroea decorticans* (Fam. Leguminosae). The shrub stratum is composed of *Larrea divaricata* (Fam. Zygophyllaceae), *Capparis atamisquea* (Fam. Capparidaceae), *Atriplex lampa* (Fam. Chenopodiaceae), accompanied by *Lycium chilensis* (Fam. Solanaceae) and *Verbena aspera* (Fam. Verbenaceae). The herbaceous stratum consists primarily of several grasses such as *Digitaria californica*, *Pappophorum caepistosum*, *Aristida mendocina* and *Setaria leucopila* (Fam. Graminae) (Roig 1971).

2) *Creosotebush community*: High density and cover of *Larrea cuneifolia* (Fam. Zygophyllaceae) characterise this habitat. The herbaceous stratum has grasses such as *Trichloris crinita* (Fam. Graminae), *Scleropogon brevifolius* (Fam. Graminae) and *Bacharis pringraea* (Fam. Compositae) and only isolated trees represent the arboreal stratum.

3) *Sand dunes*: In this habitat two strata stand out, a shrub layer dominated by *L. divaricata* and *Ximenia americana* (Fam. Olacaceae), and an herbaceous one with *Solanum euacanthum* (Fam. Solanaceae), *Gomphrena martiana* (Fam. Amaranthaceae), *Hyalis argentea* (Fam. Compositae), *Panicum urvilleanum* (Fam. Graminae) and *Portulaca grandiflora* (Fam. Portulacaceae), among other species. Occasionally, scattered specimens of *P. flexuosa* and *G. decorticans* can be observed forming a third layer (Roig 1971).

In order to characterise vegetation physiognomy at the study area during the small mammal trapping (see below), microhabitat variables were measured at 4-m^2 plots around each trap station. We recorded tree cover, total shrub cover, cover of shrubs (including *L. cuneifolia, L. divaricata, A. lampa, Condalia microphylla, C. atamisquea*, and *G. decorticans*), cover of subshrubs 5–100 cm high (*L. chilensis, L. tenuispinosum, Acantholippia seriphioides*, and *Verbena seriphioides*), herbaceous cover (species of Graminae, Compositae, Malvaceae, Solanaceae, Plantaginaceae, and Hydrophilaceae), litter cover, percentage of bare soil, foliage density, height of the highest shrub layer, and distance to the nearest shrub or tree. Each of these variables was measured independently. Principal component Analysis (PCA) was conducted to examine which combinations of variables are most predictive in describing habitat structure. All percent variables were arcsine transformed (Zar, 1984). For measuring habitat heterogeneity, Shannon and Wiener's diversity index ($H' = -\Sigma\, p_i \ln p_i$), was used including the variables of coverage (bare soil, tree cover, shrub cover, subshrub cover, and herb cover). Thus, p_i represents the proportion of each variable in relation to the total cover.

SMALL MAMMAL COMMUNITIES

The study was conducted between June 1999 and April 2001, including one winter, two springs, and two autumns. The small mammals (< 100 g) living in the Reserve are *Eligmodontia typus, Calomys musculinus, Akodon molinae, Graomys griseoflavus* (Rodentia, Muridae) and *Thylamys pusillus* (Didelphimorphia, Didelphidae) (Contreras 1979, Tognelli *et al.* 2001).

Two grids (A and B) were set in all three habitats, in seven-by-seven configuration, with 15-m intervals between sampling stations (total grid area: 0.81 ha). Mesquite forest grids were separated by 500 m, creosotebush community grids by 100 m, and sand dunes grids by 110 m. We considered the grids as replicates since each individual was marked and we did not capture marked animals from another grids. Sherman live traps were placed at each station, totalling 49 traps per grid. Traps were baited with rolled oats at sunset, and examined early in the morning for 3 consecutive days in every season. During the fall and winter months, paper strips were placed inside traps to prevent mortality by cold. Animals captured were identified, marked and released after recording trap station, weight, sex, and reproductive condition.

Diversity of small mammals in each habitat was estimated by the Shannon and Wiener index (Magurran 1988). Indices were compared among habitats using the *t* test for significant differences [calculated as $t = H'_1 - H'_2/(\sigma^2_1+\sigma^2_2)^{1/2}$, and degrees of freedom as $df = (\sigma^2_1+\sigma^2_2)^2/[(\sigma^2_{H1})^2/N_1+(\sigma^2_{H2})^2/N_2]$ Zar 1984, Magurran 1988]. Because this procedure makes pairwise comparisons only, and there were three contrasts (mesquite forest-creosotebush community; mesquite forest-sand dunes and creosotebush community-sand dunes), the Bonferroni procedure (Byrkit 1987) was used to adjust the level of significance to $p = 0.017$, thus reducing the probability of a Type I error. In addition, comparisons between grids within each habitat were also made using *t* test.

Total numbers of captured individuals of each species were compared between habitats by means of the Poisson Regression, assessing the significance of the main factors (species and habitat), and their interaction (Crawley 1993). The values of each grid were used as replicates. Because the residual errors in the analysis showed overdispersion (*i.e.*, the variance of the residuals was significantly higher than that predicted by the Poisson distribution), data were rescaled to correct for biases in the statistical test of hypotheses (Crawley 1993), using *F* tests instead of χ^2 as a measure of fit. The species showing the highest number of individuals in each habitat was considered as dominant in that environment.

In order to examine temporal variation throughout the study period, we estimated the population size of the species for each season following Krebs (1966), based on the minimum number of known animals alive (MNA). In this method the number of individuals captured (with new or previous marks) and individuals not captured but previously marked and caught in a subsequent season are counted. Data expressed as MNA were subjected to Poisson Regression, using 'season' as the variable nested within the main factor 'species'. This analysis enabled us to isolate the season effect for every mammal species and to compare their population sizes during the study period.

RESULTS

HABITAT HETEROGENEITY

Mean and standard deviation for each habitat variable is shown in Table 1.

The most heterogeneous habitats were the mesquite forest ($H'_A = 1.34$ and $H'_B = 1.39$ for grids A and B), and the creosotebush community ($H'_A = 1.32$ and $H'_B = 1.22$), whereas sand dunes represented the least heterogenous habitat ($H'_A = 1.11$ and $H'_B = 1.04$).

The PCA results reveal that PC1 accounted for 72 % of the variability and reflects the openness of the habitat. PC1 was defined mostly from cover of shrubs, litter, distance to nearest shrub and bare soil (eigenvectors are given in Table 2); PC2 explained 28% of the variability and was defined mainly from trees and herbaceous cover. Sand dune habitat was associated with high percentage of bare soil and greatest distance from the trap station to the nearest shrub (Fig. 1), whereas creosotebush was associated with high cover of

TABLE 1. – Mean and SD of cover variables recorded in each habitat.

	Mesquite forest	**Creosotebush community**	**Sand dunes**
Bare soil	70.1 ± 17.5	62.5 ± 21.6	76.4 ± 13.3
Tree cover	11.1 ± 27.8	0.13 ± 1.47	4.57 ± 18.8
Total shrub cover	48.1 ± 28	51.4 ± 28.6	30.9 ± 28.3
Shrub cover	38.1 ± 30.7	43.4 ± 29.3	25.8 ± 29.5
Subshrub cover	17.8 ± 20.5	16.8 ± 21.2	7.41 ± 14.3
Herbaceous cover	37.6 ± 21.7	47.6 ± 21.4	39.1 ± 21.5
Litter cover	75 ± 27.9	82.3 ± 25.2	71.3 ± 27.4

TABLE 2. – Eigenvalues for the first (PC1) and the second (PC2) principal components.

Variables	**PC1**	**PC2**
Bare soil	– 0.38	0.18
Tree cover	– 0.09	0.61
Shrub cover	0.39	0.05
Subshrub cover	0.35	0.29
Herbaceous cover	0.24	– 0.5
Litter cover	0.37	– 0.23
Foliage density	0.31	0.38
Distance to the nearest shrub	– 0.39	0.02
Height of the highest shrub layer	0.36	0.25

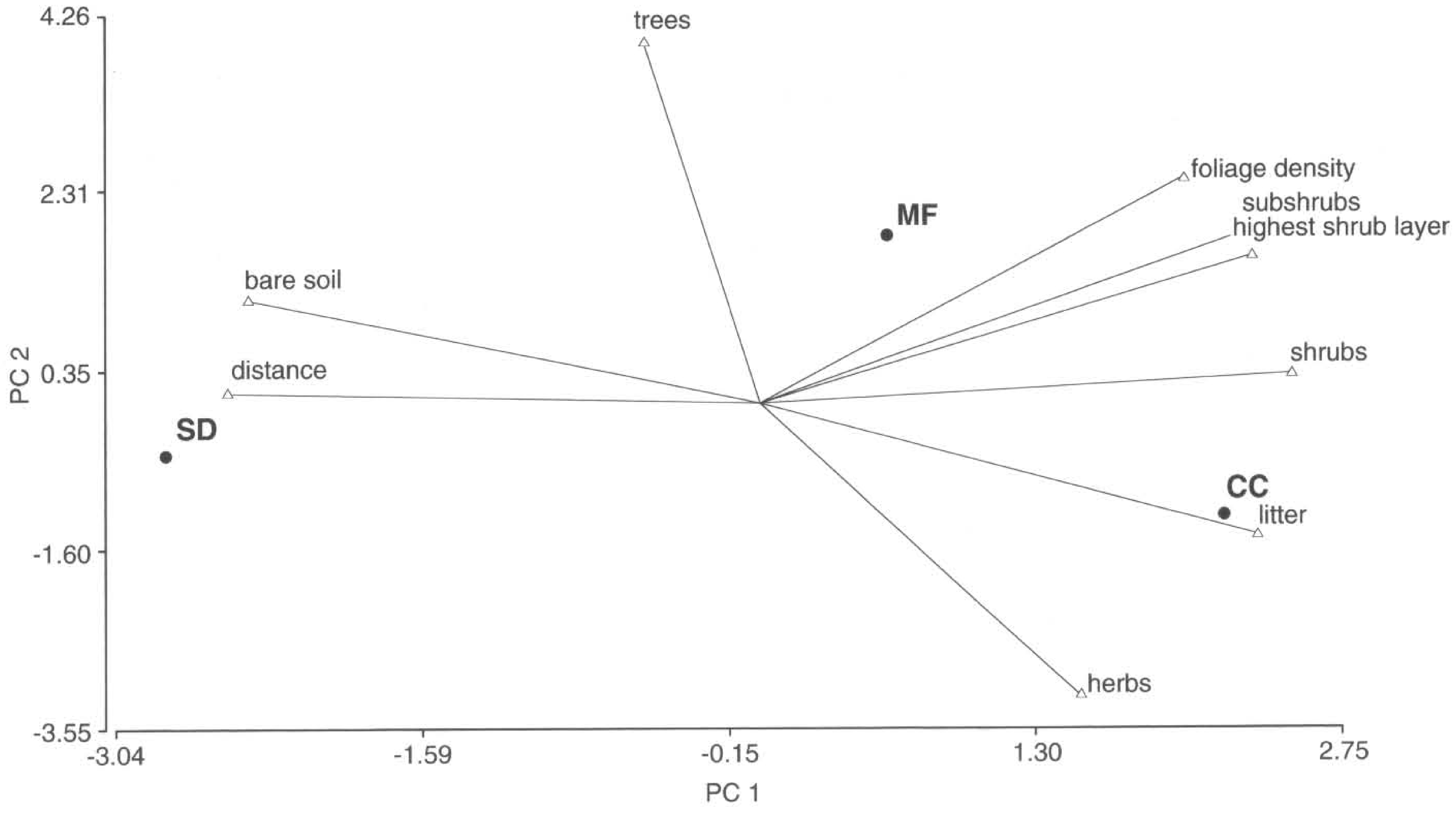

FIG. 1. – Biplot of habitats and vegetation variables resulting from a PCA. MF: Mesquite forest; CC: Creosotebush community; SD: Sand dunes.

TABLE 3. – Diversity indices and differences between grids in each habitat of the Reserve of Ñacuñán.

	Shannon index				
Habitat	**Grid A**	**Grid B**	***t* value**	**df**	***p***
Mesquite forest	1.23	1.34	1.27	139	0.2
Creosotebush community	1.42	1.32	2.14	228	0.033
Sand dunes	0.98	0.69	1.4	92	0.16

shrubs, litter and herbs. The mesquite forest was associated with high tree cover, shrub layer, subshrub cover and foliage density.

SMALL MAMMALS

A total of 497 individuals of 5 species were caught in 4410 trap-nights. These includes 156 *E. typus,* 131 *G. griseoflavus*, 126 *A. molinae*, 80 *C. musculinus*, and 4 *T. pusillus*; (Mean body size of adult specimens was 17.87 g in *E. typus*, 18.75 g in *T. pusillus*, 22.60 g in *C. musculinus*, 38.75 g in *A. molinae*, and 56.90 g in *G. griseoflavus*).

All small mammal species were captured in all habitats. The creosotebush community showed the highest total small mammal diversity (H' = 1.4) followed by the mesquite forest (H' = 1.3), and finally by sand dunes (H = 0.9). Differences in total diversity were found between the mesquite forest and sand dunes (t = 3.5; df = 133; p < 0.001), and between the creosotebush community and sand dunes (t = 4.69; df = 105; p < 0.001), but there were no significant differences between the creosotebush community and the mesquite forest (t = 1.98; df. = 232, p = 0.05). There were no significant differences in diversity indices between the two grids of the mesquite forest or between those of sand dunes, but we did find differences in diversity between the grids of the creosotebush community (Table 3).

In order to assess an association between habitat heterogeneity and small mammal diversity, we performed a simple linear regression between these variables. Using the data from each grid, the regression model showed a significant positive relationship between habitat heterogeneity and small mammal diversity (R^2_{adj}. = 0.72; p = 0.02; n = 6).

SPATIAL VARIATION

Differences among habitats were also reflected in the number of individuals (F = 15.28; df. = 2,15; p < 0.001). For all species combined, the creosotebush community had more individuals than

TABLE 4. – Analysis of deviance showing the parameters of the fitted model and the percentage of explained deviance.

Change	df	deviance	mean deviance	deviance ratio	F probability	R^2 %
+Species	4	210.17	52.54	20.989	0.000005	46.9
+Habitat	2	76.49	38.25	15.277	0.000241	17.1
+Spxhabitat	8	123.49	15.44	6.166	0.001285	27.6
Residual	15	37.55	2.50			
Total	29	447.705				

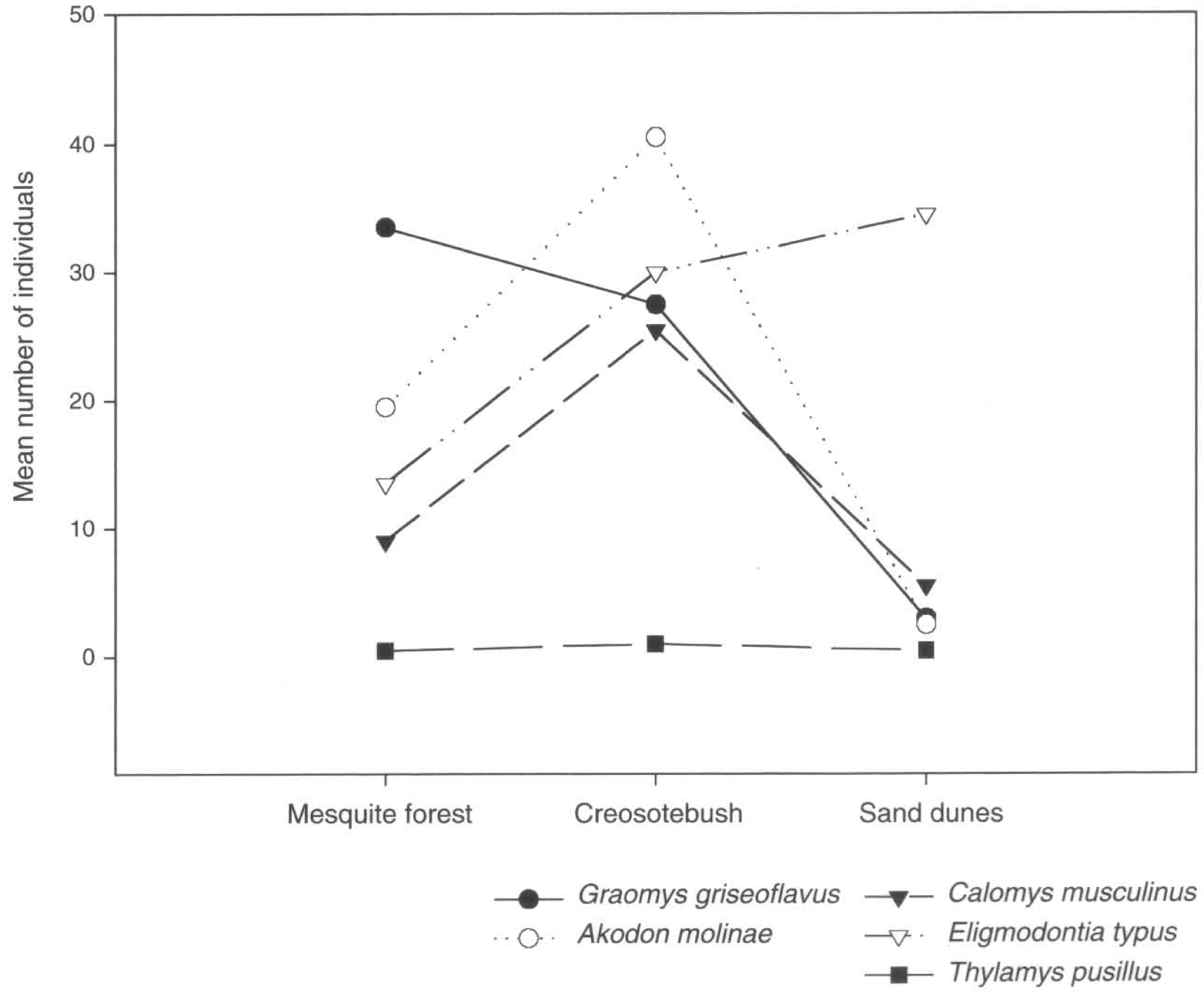

FIG. 2. – Mean number of individuals observed in each habitat during the entire sampling period in the Reserve of Ñacuñan, Argentina.

the mesquite forest (p = 0.002) and sand dunes (p < 0.001), and the mesquite forest had more individuals than sand dunes (p = 0.016). The species-habitat interaction was significant (F = 6.17; df. = 2,15; p < 0.01), indicating that some species were more frequently captured in a particular habitat (Fig. 2). The adjusted model (species + habitat + species × habitat) accounted for more than 90% of the total deviance (Table 4).

On analysing the data on mammal species in each habitat, we found that in the creosotebush community none of the small mammal species showed a clear dominance. *Thylamys pusillus* was the least captured species (p < 0.05 for all comparisons), whereas there were no differences among the rest of species (Fig. 2). In the mesquite forest, *G. griseoflavus* was captured more than *C. musculinus*, *E. typus*, and *T. pusillus* (p < 0.05; Fig. 2). In sand dunes, *E. typus* was captured more, since its numbers were significantly greater than the remaining species (p < 0.05 for all comparisons).

In comparing the number of individuals of each species among habitats, we found that *A. molinae*

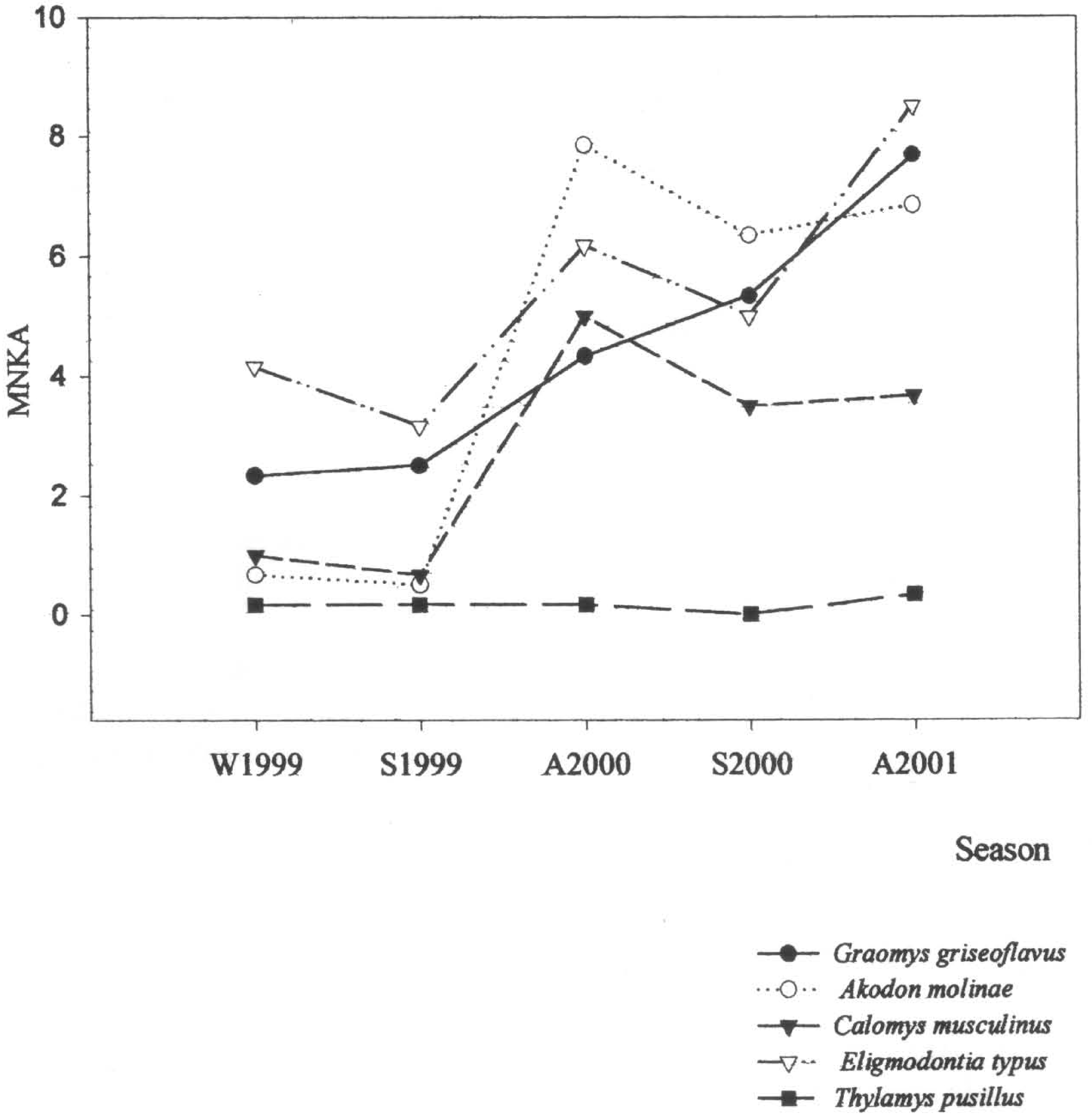

FIG. 3. – Temporal variation in abundance of all five species of small mammals during the study period. Seasons: W: winter; S: spring; A: autumn. MNA: Minimum number of known animals alive.

and *C. musculinus* were more frequent in the creosotebush community, as compare to the mesquite forest and sand dunes ($p < 0.05$ for all comparisons; Fig. 2). *Graomys griseoflavus* had similar numbers of individuals in the mesquite forest and the creosotebush community, but it was significantly less captured in sand dunes (Fig. 2). *Eligmodontia typus* had more captured individuals in the creosotebush community and sand dunes than in the mesquite forest ($p = 0.046$ and $p = 0.02$, respectively), whereas *T. pusillus* did not show differences in the number of captures among habitats.

TEMPORAL VARIATION

Population size varied greatly for all species according to season during the study period as is clearly shown in Fig. 3. The season variable was highly significant ($F = 10.37$; df = 4,14; $p < 0.001$), but not the 'speciesxseason' interaction, indicating that all species varied in the same way during the sampling dates. The highest abundance of small mammals occurred in autumn 2000, autumn 2001, and spring 2000 with respect to winter 1999 and spring 1999 ($p < 0.01$ for all comparisons; Fig. 3).

DISCUSSION

Although species richness was the same in all habitats, as predicted, the highest diversity of small mammal species was found in more heterogeneous habitats such as the mesquite forest and creosotebush community. In general, desert ecosystems support a few species at the same site. In North American deserts, 80% of the sampled sites were occupied by combinations of two to five small mammal species (Brown & Kurzius 1987). A similar situation was reported by Kelt *et al.* (1996) when comparing deserts of the world [North America, South America (Altiplano), Australia, and greater Eurasia], and by Streilein (1982) for Brazilian Caatinga. Our results agree with the pattern reported by these authors, since five small mammals coexisted in each habitat during the peak of population density, whereas only one or two species were present in times of low density.

We found that the species inhabiting the Central Monte Desert (i.e., Biosphere Reserve of Ñacuñán) make a differential use of space. All species were captured in the three habitats, but their relative abundance underwent notable variations among them. There was a clear avoidance of open areas (sand dunes) by *G. griseoflavus*, *C. musculinus* and *A. molinae*, whereas *E. typus* was the dominant species in this habitat. This is supported by an early study on fire disturbances in the Reserve that indicates that the only species that monopolized the habitat after one year was *E. typus*, and that this is correlated with a decrease in vegetational heterogeneity (Ojeda 1989). However, in the present study *E. typus* did not discriminate between sand dunes and creosotebush, since the total number of individuals was similar for both habitats. The ecomorphological attributes of *E. typus* (elongated hind legs, saltatorial locomotion; Mares 1975) could be advantageous for this species in exploiting habitats of low plant cover and sandy soils, due to greater predator avoidance. Although *E. typus* is capable of exploiting different habitats in the Reserve, it becomes dominant where habitat conditions are less favourable for species with different morphological attributes.

Graomys griseoflavus has been reported as a species capable of occupying xeric habitats, cultivated fields, sandy areas with rocks, and riparian forests (Redford & Eisenberg 1992). Gonnet & Ojeda (1998) also found that this species used a greater diversity of habitats in the Andean foothills. In the Reserve of Ñacuñán, the number of captures of *G. griseoflavus* was the same for the creosotebush community and for the mesquite forest, but this species was dominant in the latter habitat. This species has the ability to climb (Mares 1977) and areas with high cover of trees seem be the preferred habitat for *G. griseoflavus*. This has been the only species captured in trees (Bender & Tabeni, *pers. com.*) and its diet in the Reserve is mainly leaves of *Prosopis* sp. (Campos 1997, Campos *et al.* 2001). *A. molinae*, in contrast, is associated with high cover of shrubs and grasses (Corbalan & Ojeda 2001; Navarro, 1991). *A. molinae* and *C. musculinus* were captured more in the dense vegetation of the creosotebush habitat as expected from their biological attributes. The high cover of shrubs and herbs, and the low proportion of arboreal habitat for raptors may provide all species with a safe habitat from predators.

The common opposum *T. pusillus* is an insectivorous semiarboreal species. The type of bait used and/or the location of traps were probably the cause for the low number of captures of this species. This low capture rate prevented drawing conclusions on their habitat associations and population fluctuations.

Spatial and temporal variability have been reported for other deserts (e.g. Chihuahuan desert; Whitford 1976, Brown & Zeng 1989). In this study all species showed variations in density throughout the year, and in several periods they were not captured. Autumns (beginning of dry season of 2000 and 2001) and the spring of 2000 (beginning of wet season) appear to be the periods of highest population abundance. The high abundance of small mammals in April-May (autumn) could be attributable to the recruitment of juveniles, that were born in months of higher food availability such as grass, seeds, fruits and insects. In our study site, grasses are sensitive to light rains, starting their vegetative phase early in the wet season (September) (Dalmasso 1994, Rossi 1994). The same is true for *L. tenuispinosum* and *L. chilensis*, whose reproductive periods appear to be closely associated with precipitation due to their shallow root systems (Rossi 1994). The fruit production of *C. atamisquea*, *C. microphylla* and *L. tenuispinosum* is important in the summer months, and fruit availability continues until March-April (Rossi 1994). In addition, the abundance and diversity of insects in the area is higher in spring and early summer (Debandi 1999, 2000, Roig-Juñent *et al.* 2001).

CONCLUSIONS

In conclusion, the small mammal assemblages of the Monte Desert are dynamic in time and in space. Avoidance of open areas by all species except *E. typus* indicates that habitat variables (e.g., tree cover, shrub cover, herb cover, openness) are among the main factors influencing their distribution and assemblage structure, as in other deserts. Thus, habitat heterogeneity, diet, body size, and intra- and inter-specific relationships could influence and facilitate the coexistence of species within each habitat. However, the ultimate mechanisms of coexistence are still unknown and should be approached through detailed field experiments.

Many ecological studies on deserts are conducted in short periods of time, with little disregard of habitat heterogeneity. Our results strongly suggest that both the temporal and the spatial variability should be taken into account in studies of animal communities in desert ecosystems.

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