

J.R. Gutiérrez · P.L. Meserve · S. Herrera
L.C. Contreras · F.M. Jaksic

Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone

Received: 22 April 1996 / Accepted: 14 August 1996

Abstract We monitored the cover and seed bank response of shrubs, perennial herbs, and ephemeral plants to experimental exclusion of both the principal rodent herbivore, *Octodon degus*, and its vertebrate predators from 1989 to 1994 in a semiarid Chilean mediterranean site. Although both richness and species composition of the plant community at the study site were largely determined by abiotic factors (mainly rainfall and soil nutrients), predator and herbivore exclusion had significant effects on the relative abundance of several plant species. Experimental exclusion of herbivores was associated with increased cover of some shrubs and a perennial grass, and decreased cover and seed densities of several ephemerals, especially those exotic or restricted to areas underneath shrubs. Herbivores apparently reduced shrubs through browsing and indirectly affected herb cover and seed densities by opening up areas under shrubs and/or modifying physical and chemical conditions of the soil. Plant responses to predator exclusion were less clear. Nevertheless, higher cover of some shrubs and ephemerals in the presence of predators suggests tritrophic effects through changes in small mammal densities and/or foraging behavior.

Key words Herbivory · Predation · Tritrophic effects · Ephemeral plants · Chilean semiarid zone

Introduction

Environmental stress and climatic variability have traditionally been cited as the primary determinants of species richness and plant abundance in arid and semiarid zones (Noy-Meir 1973; Beatley 1974; Ludwig and Whitford 1981). In the last decade, however, a number of studies have shown that small mammals can have significant effects on the plant community (Huntly and Inouye 1988; Whickler and Detling 1988; Brown and Heske 1990; Martinsen et al. 1990; Swihart 1991; Samson et al. 1992; Heske et al. 1993). These effects may be a direct result of plant consumption by small mammals, or an indirect consequence of physical disturbance due to their activities (Contreras and Gutiérrez 1991; Whitford 1993). Further, these effects may be mediated by predators, which may indirectly affect plant composition and abundance by changing the density and/or behavior of small mammals (Jaksic 1986).

Previous studies of Chilean mediterranean-type ecosystems suggested a major role of predation on small mammals (e.g., Jaksic et al. 1979, 1981, 1992, 1993), and a major effect of small mammal herbivores on plants (Fuentes and Le Boulengé 1977; Jaksic and Fuentes 1980; Fuentes et al. 1983, 1984). However, few long-term field experiments have been conducted in the temperate Neotropics, and such studies are necessary to assess the generality of patterns largely derived from studies conducted in the Northern Hemisphere (Davidson et al. 1985; Brown et al. 1986; Brown and Heske 1990; Samson et al. 1992; Heske et al. 1993, 1994). Since 1989, we have been conducting a long-term manipulation at a semiarid site in north-central Chile, investigating the role of biotic interactions in small mammal and plant assemblages. We have used fences and netting to selectively exclude mammalian and avian predators, and the principal small mammal herbivore, the degu (*Octodon degus*), from large, replicated plots (see Meserve et al. 1993a, b for details). Jaksic et al. (1993) showed that this ecosystem has a diverse predator assemblage for which small mammals are the most important prey, thus

J.R. Gutiérrez (✉) · S. Herrera
Departamento de Biología Universidad de La Serena,
Casilla 599, La Serena, Chile

P.L. Meserve
Department of Biological Sciences, Northern Illinois University,
DeKalb, IL 60115, USA

L.C. Contreras
CONAMA, Casilla 520-V, Santiago, Chile

F.M. Jaksic
Departamento de Ecología, Pontificia Universidad Católica de
Chile, Casilla 114-D, Santiago, Chile

suggesting a major role of predation. Numbers and survival of the principal small mammal species (*O. degus* and *Phyllotis darwini*) were significantly higher on predator exclusion plots (Meserve et al. 1996). Herein we describe the cover and soil seed number responses of shrubs, perennial herbs, and ephemeral plants to the experimental exclusion of both the principal herbivore (the degu) and vertebrate predators over a 6-year period (1989–1994).

Materials and methods

Research site

The study area is located in Parque Nacional Fray Jorge (71°40'W, 30°38'S) c. 100 km south of La Serena and 400 km north of Santiago, Chile, near the coast. This 10000-ha park contains semiarid thorn scrub vegetation, and isolated fog forests (on coastal mountain ridges), which have been protected from grazing and disturbance since 1941. The climate is semiarid mediterranean with 90% of the mean 85 mm annual precipitation falling in winter months (May–September); summer months are warm and dry. After a normal rainfall year in 1989 (89 mm), and a dry year in 1990 (32 mm), 1991 and 1992 were wet (233 mm, and 229 mm, respectively), 1993 was close to average (77 mm) and 1994 was a dry year (35 mm).

The plant community of the study area (Quebrada de las Vacas, 240 m elevation) is characterized by spiny drought-deciduous and evergreen shrubs 2–3 m in height, with an herbaceous understory, and generally unvegetated sandy areas between shrubs. The growing season of the most abundant shrubs extends from August to December (spring season). This community has been termed the *Portleria chilensis-Adesmia bedwellii-Proustia pungens* association (Muñoz and Pisano 1947). Of the dominant shrub species *P. chilensis* (Zygophyllaceae, 30% cover), *A. bedwellii* (Papilionaceae, 5% cover), and *Baccharis paniculata* (Asteraceae, 2% cover) are evergreen, *Chenopodium petiolare* (Chenopodiaceae, 20% cover) is a suffruticose perennial shrub with persistent foliage found in the understory and periphery of shrubs, and *Proustia pungens* (Asteraceae, 6% cover) is a drought-deciduous species. A complete account of plant species composition and abundance at the site is provided in Gutiérrez et al. (1993a).

Year-round members of the small mammal assemblage include the rodents (*Octodon degus* (degu), *Akodon olivaceus* (olivaceous field mouse), and *Phyllotis darwini* (leaf-eared mouse)). Other rodents such as *Oligoryzomys longicaudatus* (long-tailed rice rat), *Abrothrix longipilis* (long-haired field mouse), *Abrocoma bennetti* (chinchilla rat), and the marsupial *Thylamys elegans* (mouse opossum) were sporadic and/or uncommon in occurrence (Meserve et al. 1995, 1996). The three commonest small mammals have different feeding niches: *Octodon degus* is an herbivore, *P. darwini* a granivore-herbivore, and *Akodon olivaceus* an omnivore. A second, less abundant species is present for each of these three trophic specializations (*Abrocoma bennetti*, *Oligoryzomys longicaudatus* and *Abrothrix longipilis*, respectively; Meserve 1981a).

The more prominent vertebrate predators include owls (*Speotyto cunicularia*, *Tyto alba*, *Bubo virginianus*, and *Glaucidium nanum*), and the culpeo fox (*Pseudalopex culpaeus*); small mammals are major prey for most of them (Fulk 1975; Jaksic et al. 1993). Predator concentrations within the park are particularly high, because it is one of the only significant areas of undisturbed semiarid scrub in north-central Chile.

Methods

During January–March 1989, sixteen 75×75 m plots (0.56 ha) were delineated in homogeneous habitat within the valley at least

50 m from each other, and randomly assigned to treatments as follows:

1. Four plots had low (1.0 m high) fencing buried c. 40 cm into the ground with enlargements of the 2.5-cm mesh cut in the chicken wire (yielding c. 5-cm diameter holes) at ground level every 2 m, yielding a total of 159 5-cm holes for each plot, to allow access to all small mammals and predators (hereafter referred to as control plots or +D +P plots).
2. Four plots had high (1.8 m high) fencing buried 40 cm, a 1-m-high overhang, polyethylene netting (c. 15-cm mesh) overhead, and 5-cm holes in the fencing to exclude predators, but allow small mammal access (including degus; +D –P plots).
3. Four plots had low (1.0 m high) fencing buried 40 cm deep to exclude the principal small mammal herbivore, the degu, but not other small mammals or predators (–D +P plots).
4. Four plots had high (1.8 m high) fencing buried 40 cm deep, overhangs and netting that excluded both degus and predators (–D –P plots).

For statistical purposes, the experiment is a 2×2 factorial design with treatments being predation (presence or absence) and herbivory (presence or absence of degus).

Three procedures for monitoring plant community changes were used. To determine shrub and perennial herbaceous cover, four permanent parallel lines (each 75 m long) located 15 m apart were used in each plot; each line had 150 points at 50-cm intervals. These lines were sampled every 4 months in 1989 and every 3 months from 1990 on, using the point intercept technique (Mueller-Dombois and Ellenberg 1974). To measure the cover of annuals and geophytes, the point intercept technique was applied to ten randomly located 1.5-m-long segments (subdivided into 30 points at 5-cm intervals) along the permanent lines every month during the growing season (winter-spring seasons). Twenty soil samples per plot were randomly collected every 4 months beginning in April 1989 using a 35.4-cm³ collecting tube (3 cm diameter×5 cm depth). Previous sampling to 6 cm demonstrated that less than 10% of the seeds are found in the 4–6 cm interval (Meserve 1981b). Samples were returned to the laboratory, separated by mechanical sieving, and identified to species whenever possible using seeds collected from plants in the field as a reference.

Both single and double within-subject repeated measures analysis of variance (rmANOVA; PROC ANOVA; SAS 1988) were used to analyze plant cover and soil seed number responses to the treatments (von Ende 1993). Between-subject factors were predation and herbivory (degu); within-subject factors were year and month. Between- and within-subject interactions were also examined. Plant cover data were arcsine squared-root transformed previous to statistical analysis. Due to increased sampling effort for perennial plants after 1989, only data from 1990–1994 were analyzed for treatment effects. Because the start and extent of the growing seasons for ephemerals differed between years, we used only one cover value/year, selecting the month in each year when the majority of species reached their peak cover. Seed sample data were pooled within plots. All *P* values for within-subjects analyses were Huynh-Feldt adjusted, a procedure that corrects for deviations in the sphericity assumption of the variance-covariance matrix (von Ende 1993), and considered significant at $\alpha \leq 0.05$. To determine treatment effects at the community level, rmANOVAs were run on total cover and seed numbers of shrubs+perennial herbs and ephemeral plants (annuals+geophytes). We also calculated Shannon-Wiener (H') diversity indices per treatment per year using abundances derived from cover values for both groups of plants. Plant species were also grouped according to the life-forms defined by Raunkiaer (Whittaker 1975), which considers the relation of the perennating tissue to the ground surface.

To determine treatment effects at the species level, rmANOVAs were run on plant species. Because of the large number of rare species, only those with cover >1% and present in the plots for at least 4 years were included in the analyses. This considerably reduced the number of analyses. Scheiner (1993) recommends that when more than one response variable is measured, the most appropriate method of analysis is usually multivariate analysis of variance (MANOVA). However, the low number of replicates used

in our study and the high number of levels of within-subject factors (time and plant species) seriously restrict the power of MANOVA (von Ende 1993), thus precluding its use here.

Results

Perennial plants

Numbers of perennial plant species were 17 in 1989, 15 in 1990, and 20 for 1991–1994. Total perennial cover on the control plots ranged from 59 to 67% in 1989, 50–64% in 1990, 48–62% in 1991, 48–62% in 1992, 47–63% in 1993, and 39–58% in 1994. These figures are similar to those (58–60% cover) reported for the same site 50 years earlier (Muñoz and Pisano 1947).

To date, there have been no significant treatment effects on overall perennial cover (Table 1). However,

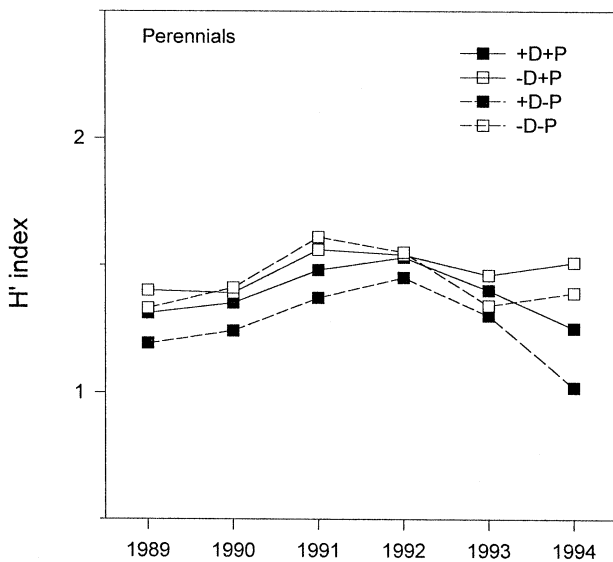


Fig. 1 Shannon-Wiener's index (H') for perennial plants on degu+predator open (+D +P), degu-exclusion (-D +P), predator-exclusion (+D -P), and degu+predator exclusion (-D -P) plots

treatments seem to have a long-term effect on species diversity of perennials, which is only evident in 1994 (Fig. 1) with greater diversity in -D than in +D plots. Among life-forms, only chamaephytes showed a marginally significant degu effect ($F_{(1,12)}=4.70$; $P=0.0511$)

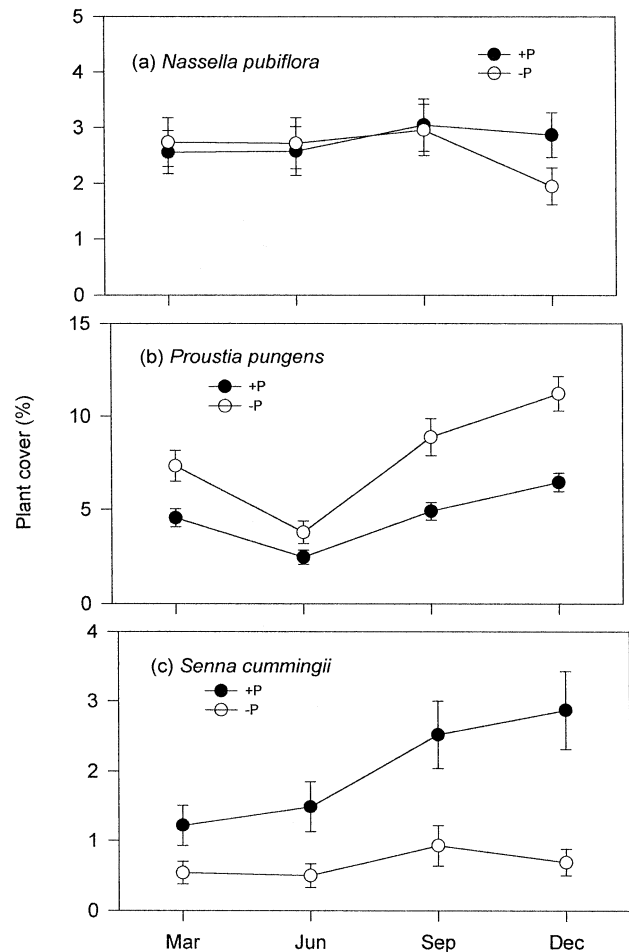


Fig. 2 Seasonal plant cover (mean±1 SE) trends of **a** *Nassella pubiflora*, **b** *Proustia pungens*, and **c** *Senna cummingii* on predator-open (+P) and predator exclusion (-P) plots

Table 1 F values for repeated measures ANOVAs of shrub and perennial herb plant cover with significant differences in Fray Jorge during 1990–1994 (factors are: P predator, D degu, Y year,

M month). Within subject P -values are H-F adjusted. Columns Y , M , and $Y \times M$ have been omitted from the table

Species	df	P 1,12	D 1,12	$P \times D$ 1,12	$Y \times P$ 4,18	$Y \times D$ 4,18	$Y \times P \times D$ 4,18	$M \times P$ 3,36	$M \times D$ 3,36	$M \times P \times D$ 3,36	$Y \times M \times P$ 12,144	$Y \times M \times D$ 12,144	$Y \times M \times P \times D$ 12,144
<i>Anisomeria littoralis</i>		3.59	0.06	0.66	1.19	0.21	4.06**	1.06	2.92*	1.28	1.59	0.92	1.72
<i>Baccharis paniculata</i>		0.00	5.64*	1.21	0.28	0.75	1.57	0.11	0.67	0.53	0.93	1.85	1.04
<i>Chenopodium petiolare</i>		0.00	3.16	0.05	1.79	1.20	0.69	2.01	0.83	8.12**	0.39	1.40	0.37
<i>Nassella pubiflora</i>		0.17	0.06	0.65	0.31	2.38	1.64	4.09*	3.95*	3.43*	0.77	1.14	1.33
<i>Proustia pungens</i>		5.38*	0.22	0.19	0.60	1.38	0.74	3.31*	0.48	2.68	0.49	0.77	1.36
<i>Senna cummingii</i>		2.26	0.15	0.43	1.77	0.53	0.88	4.75**	0.43	0.94	1.30	1.26	0.52
Chamaephytes		0.02	4.70	0.62	1.90	0.40	0.54	2.05	0.47	3.57*	0.99	1.09	1.13
Hemicryptophytes		0.16	0.02	0.06	0.22	1.39	0.87	1.77	2.16	1.60	0.87	1.12	1.63
Phanerophytes		0.00	0.03	0.18	0.50	2.07	1.35	1.06	0.25	2.02	0.74	0.95	1.95
Total cover		0.48	0.57	0.28	2.41	0.46	2.51	1.22	0.29	1.66	0.50	1.00	0.71

* $P < 0.05$, ** $P < 0.01$

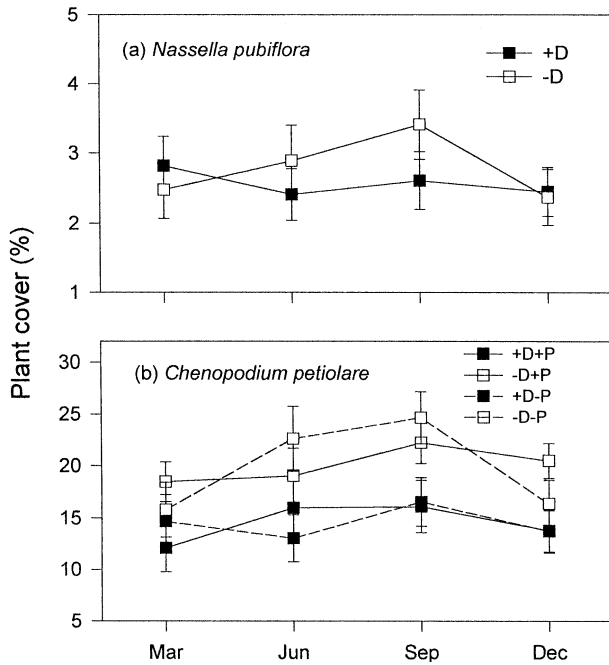


Fig. 3 Seasonal plant cover trends (mean±1 SE) of **a** *Nassella pubiflora* on degu-open (+D) and degu-exclusion (-D) plots and **b** *Chenopodium petiolare* on degu×predator interaction plots; symbols as in Fig. 1

Table 2 F values for repeated measures ANOVAs of ephemeral plant cover with significant differences in Fray Jorge during 1989–1994 (factors are: P predator, D degu, Y year, M month). Within subject P-values are H-F adjusted. Column Y has been omitted from the table

Species	df	P	D	P×D	Y×P	Y×D	Y×P×D
<i>Adesmia tenella</i>		5.47*	0.52	0.19	3.40*	0.64	0.50
<i>Camissonia dentata</i>		0.25	0.70	0.29	0.66	3.24*	0.54
<i>Moscharia pinnatifida</i>		0.44	4.16	1.40	0.47	2.23	2.25
Therophytes		0.04	2.45	0.20	1.83	6.46**	0.72
Geophytes		0.09	0.00	0.00	1.47	1.86	1.19
Total cover		0.05	1.68	0.15	1.72	6.09**	0.44

* P<0.05, ** P<=0.01

having higher cover in the degu exclusion plots (23% vs. 16%).

For species, there were several significant differences in shrub cover due to treatment effects: *Proustia pungens* had greater cover in predator-exclusion plots (8% vs. 5%), whereas *Baccharis paniculata* (2.2% vs. 0.7%) had greater cover in degu-exclusion plots. *Nassella pubiflora* (Gramineae), *Proustia pungens*, and *Senna cummingii* (Caesalpiniaceae) showed a significant month×predator interaction. *N. pubiflora* and *S. cummingii* had higher cover in the predator-open plots while the opposite was true for *P. pungens*. These differences were larger in September (early spring) and December (early summer) (Figs. 2a–c). *N. pubiflora* also showed a significant month×degu with higher cover in the degu-exclusion plots (Fig. 3a). *Cheno-*

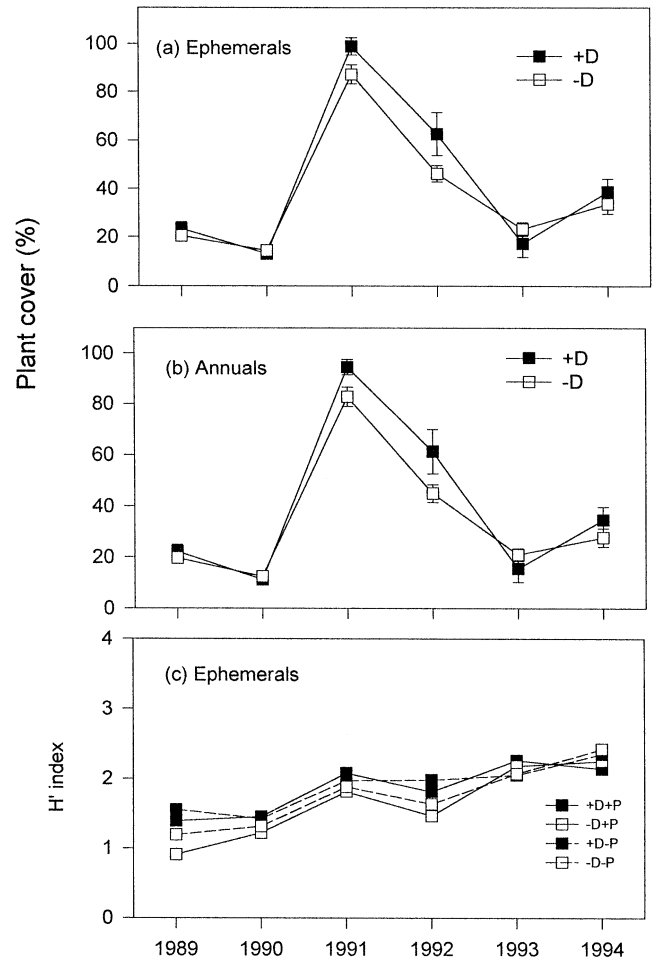


Fig. 4 Yearly plant cover trends (mean±1 SE) of **a** ephemeral and **b** annual plants on the degu-open (+D) and degu-exclusion (-D) plots. **c** Shannon-Wiener's (*H'*) for ephemeral plants on degu×predator interaction plots; symbols as in Fig. 1

podium petiolare showed a significant month×predator×degu interaction, having higher cover either in the -D -P or -D +P plots (Fig. 3b). There were other significant time×treatment interactions, but because of their unclear trends they will not be discussed here.

Ephemeral plants

During the 1989 and 1990 growing seasons 26 ephemeral species were recorded, 53 in 1991, 55 in 1992, 46 in 1993, and 50 in 1994. Total ephemeral cover in control plots decreased from 27.6% in 1989 to 14.8% in 1990, peaked at 80.0% in 1991, decreased in 1992 (54.0%), and again in 1993 (26.2%), having a small increment in 1994 (37.4%). Number of species and plant cover followed the rainfall pattern (Gutiérrez et al. 1993a).

Results for significant rmANOVAs are summarized in Table 2. Total cover of ephemeral (annuals+geophytes) and annual plants showed a significant year×degu interaction having higher cover in the degu-open plots in

Fig. 5 Yearly plant cover trends (mean±1 SE) of **a** *Adesmia tenella* on predator-open (+P) and predator-exclusion plots, **b** *Camissonia dentata*, **c** *Moscharia pinnatifida* on degu-open (+D) and degu-exclusion (-D) plots, and **d** *M. pinnatifida* on degu×predator interaction plots; symbols as in Fig. 1

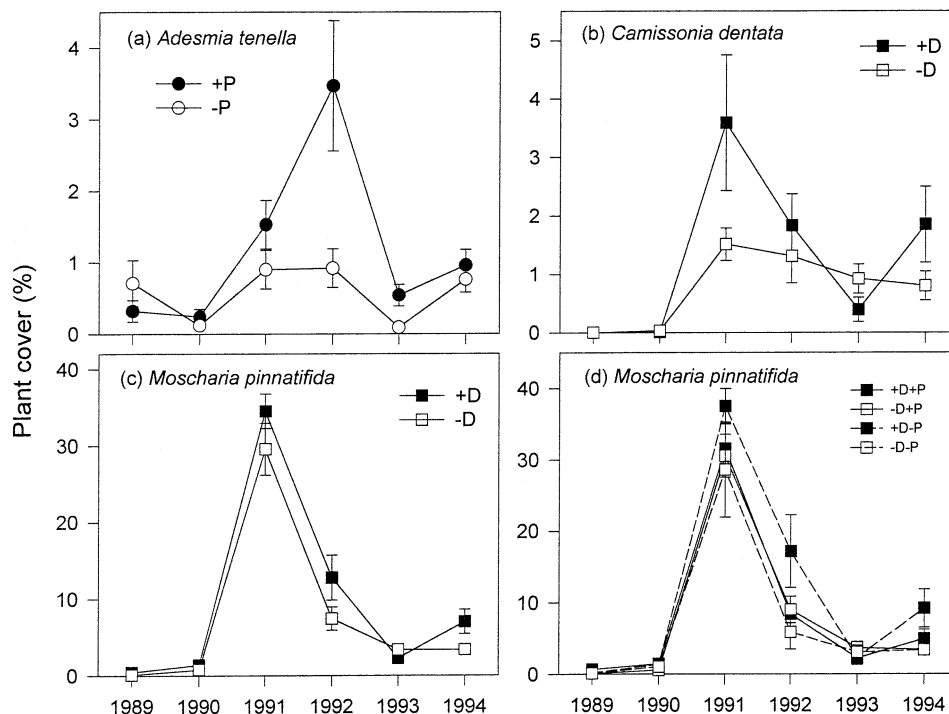


Table 3 *F* values for repeated measures ANOVAs of plant species seed densities with significant differences in Fray Jorge during 1989–1994 (factors are: *P* predator, *D* degu, *Y* year, *M* month).

Within subject *P*-values are H-F adjusted. Columns *Y*, *M*, and *Y*×*M* have been omitted from the table

Species	<i>df</i>	<i>P</i> 1,12	<i>D</i> 1,12	<i>P</i> × <i>D</i> 1,12	<i>Y</i> × <i>P</i> 5,60	<i>Y</i> × <i>D</i> 5,60	<i>Y</i> × <i>P</i> × <i>D</i> 5,60	<i>M</i> × <i>P</i> 2,24	<i>M</i> × <i>D</i> 2,24	<i>M</i> × <i>P</i> × <i>D</i> 2,24	<i>Y</i> × <i>M</i> × <i>P</i> 10,120	<i>Y</i> × <i>M</i> × <i>D</i> 10,120	<i>Y</i> × <i>M</i> × <i>P</i> × <i>D</i> 10,120
<i>Chenopodium petiolare</i>		0.58	0.66	0.35	2.12	1.00	2.27	0.50	0.12	2.97	2.40*	0.49	0.83
<i>Cryptantha dolichophylla</i>		0.58	0.17	7.79**	0.65	0.86	2.94*	2.19	1.54	1.49	1.45	0.51	0.60
<i>Cuscuta micrantha</i>		0.31	1.30	0.02	3.98**	3.56**	0.28	1.15	0.86	1.67	1.16	1.75	0.64
<i>Descurainia cumingiana</i>		0.33	0.00	4.19	2.89*	2.67	2.35	3.86*	3.08	1.32	2.33	2.23	3.13*
<i>Erodium</i> spp.		0.08	7.04*	0.03	0.58	4.99*	0.10	0.04	0.75	0.28	0.50	1.54	0.38
<i>Moscharia pinnatifida</i>		2.37	5.02*	1.48	0.24	2.22	0.22	2.47	1.79	0.88	1.51	0.94	0.51
<i>Plantago hispidula</i>		0.86	0.92	0.40	1.10	0.72	2.14	1.40	0.10	0.59	0.71	0.30	2.84*
<i>Schismus arabicus</i>		2.32	0.05	0.01	3.21*	0.83	0.92	1.33	1.39	1.42	2.11	1.27	1.57
Therophytes		0.32	5.26*	0.00	0.24	1.20	1.78	0.12	0.59	0.21	0.59	0.97	0.64
Chamaephytes		0.40	0.65	0.38	2.25	1.08	2.31	0.39	0.09	3.19	2.42*	0.51	0.84
Geophytes		0.96	0.58	0.13	0.53	0.42	1.19	1.29	1.04	1.29	0.82	1.30	0.90
Hemicryptophytes		0.00	0.55	0.68	0.37	0.29	0.67	0.15	0.27	2.15	0.56	0.58	1.51
Phanerophytes		0.36	1.58	0.12	0.63	0.84	0.70	1.07	1.03	0.17	0.43	0.83	0.59
Total		0.06	0.29	0.35	2.11	2.67*	3.59**	0.19	0.39	1.29	2.38*	0.50	0.81

* $P < 0.05$, ** $P < 0.01$

1991 and 1992 (Fig. 4a, b). However, unlike the case of perennials, treatments have not affected species diversity of ephemeral plants (Fig. 4c).

The following species showed significant year×treatment effects: *Adesmia tenella* (Papilionaceae) had higher cover in predator-open plots, with the largest differences observed in 1992 (Fig. 5a). *Camissonia dentata* (Onagraceae) had higher cover in the degu-open plots particularly in 1991 (Fig. 5b). *Moscharia pinnatifida* (Asteraceae) had marginally significant degu ($F_{(1,12)}=4.16$; $P=0.0639$), year×degu ($F_{(5,60)}=2.23$; $P=0.0633$), and year×predator×degu ($F_{(5,60)}=2.25$; $P=0.0604$) interaction

effects. Cover was higher in the degu-open and in the +D -P plots (Fig. 5c, d).

Seeds

Sixty-three taxa were identified in the soil seed bank, mostly to species level (*c.* 75% of those encountered), and numbers of species per year have ranged from 33 to 52 over 6 years. The soil seed bank was relatively less diverse during 1989 and 1990, but thereafter a significant increase occurred due to the herbaceous growth that

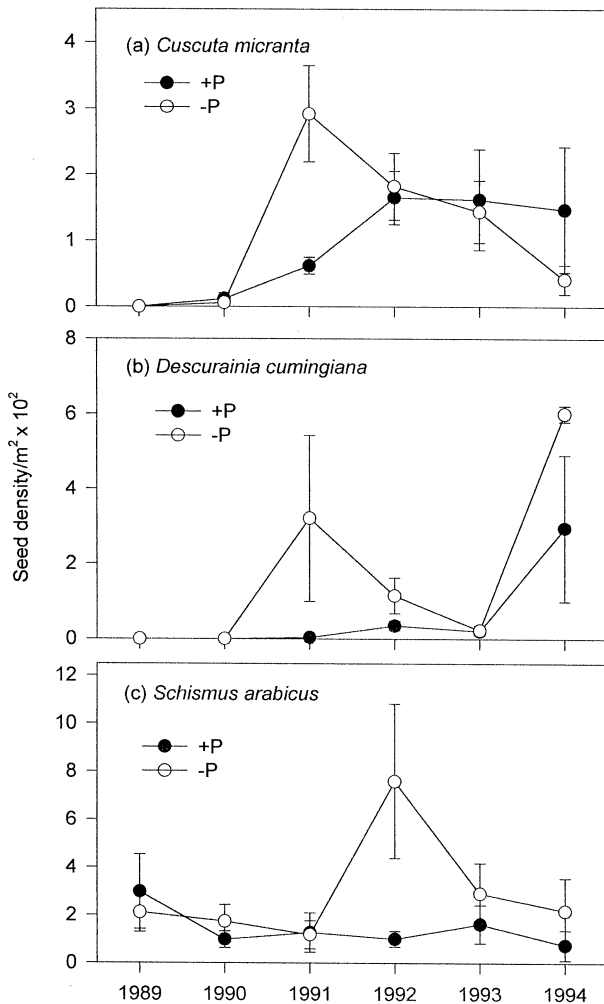


Fig. 6 Yearly seed density/m² (mean±1 SE) of **a** *Cuscuta micrantha*, **b** *Descurainia cumingiana*, and **c** *Schismus arabicus* in predator-open (+P) and predator-exclusion (-P) plots

started in 1991. Total seed densities ranged from 15011 to 41832/m², considerably higher than in 1973–1974 (10740–23930/m², Meserve 1981b). These densities, however, are well below the maximum value (over 100000/m²) reported for Sonoran Desert soils (Reichman 1984).

Seed densities were highly variable between years as well as within years but were closely associated with plant cover patterns. Higher seed densities were found in the wet years of 1991 and 1992, and in the samples taken in early summer and early autumn. Lowest seed densities were found in late winter (i.e., at the time of ephemeral plant emergence).

Significant rmANOVA results for seed analyses are summarized in Table 3. For total seed density, there were significant year×degu, year×predator×degu, and year×month×predator interactions. Chamaephytes also showed a significant year×month×predator interaction. Despite these interactions, no clear patterns could be established. Seed densities of annual herbs were higher in

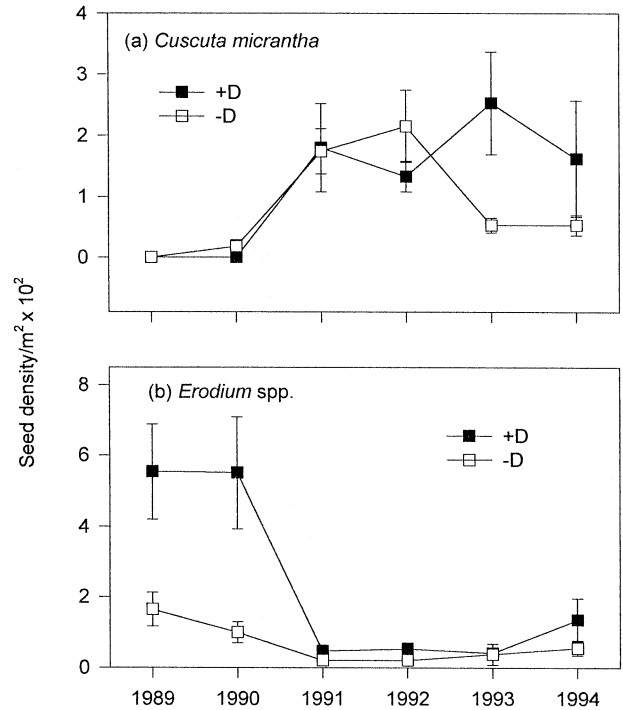


Fig. 7 Yearly seed density/m² (mean±1 SE) of **a** *Cuscuta micrantha*, **b** *Erodium* spp. in degu-open (+D) and degu-exclusion (-D) plots

the degu-open plots (12659 vs. 10209 seeds/m²). This result parallels that described for plant cover.

Among individual species, seed densities of *Erodium* spp. (Geraniaceae, 231 vs. 66 seeds/m²) and *Moscharia pinnatifida* (2128 vs. 1350 seeds/m²) were higher in the degu-open plots. Several time×treatment interactions were detected among ephemeral species, reflecting the consequences of varying precipitation. A year×predator interaction was detected for *Cuscuta micrantha* (Cuscutaceae), *Descurainia cumingiana* (Cruciferae), and *Schismus arabicus* (Gramineae). These three species had higher seed densities in the predator-exclusion plots (Fig. 6a–c). *C. micrantha* and *Erodium* spp. had a significant year×degu interaction. Both species had higher seed densities in the degu-open plots (Fig. 7a, b). Other species also showed significant time×treatment interactions, but because of their unclear trends they will not be discussed here.

Discussion

Although both richness and species composition of the plant community at the study site were largely determined by abiotic conditions (mainly rainfall and soil nutrients, Gutiérrez et al. 1993a, b), our results indicate that vertebrate predator and herbivore (degu) exclusion had significant effects on the relative abundance of several plant species.

Cover of some chamaephytes (e.g., *Anisomeria littoralis* (Phytolaccaceae), *Baccharis paniculata*, *Chenopodium petiolare*) and of the perennial grass *Nassella pubi-*

flora was higher in the degu-exclusion plots. *C. petiolare* is the most abundant species among the chamaephytes (10–20% cover, Gutiérrez et al. 1993a) and comprises up to 60% of the diet of degu at the site (Meserve 1981a). All of these species produce herbaceous green stems and branches during the growing season. Degus experimentally exposed to both new and mature leaves of different species of Chilean mediterranean shrubs prefer new growth, and do not discriminate between different shrub species (Simonetti and Montenegro 1981). This foraging behavior of degu may in part explain why cover of woody shrub species did not show any significant change when degus were excluded.

Ephemeral plants are a highly variable resource between years, depending in turn on the amount, frequency and timing of rainfall at the site. Cover varied from 15% in dry years to 80% in wet years. Meserve et al. (1984) showed that at La Dehesa, a mesic mediterranean site, near Santiago, degus consumed relatively more forb and grass foliage and seeds than at Fray Jorge, where shrub foliage, seeds, and conductive tissue were considerably more important in their diets. Both rainfall and the presence of ephemeral plants are more predictable in central than in northern Chile. Degus in semiarid north-central Chile may be more dependent on predictable resources such as perennial plants and hence, ephemeral species demonstrated no positive responses to degu exclusion. In fact, total cover of ephemeral plants and cover of the forbs *Camissonia dentata*, and *Moscharia pinnatifida* was higher in degu-open plots. Degus build burrows in shrub patches, and develop conspicuous runways as a result of their linear movements in the open areas between shrubs (Jaksic 1986; Lagos et al. 1995), which remain in the field for several years. The soil disturbance produced by degu activity may contribute to increased micro-scale spatial heterogeneity and opening up areas under bushes, thus creating areas apt to be colonized by subordinate competitors or exotic herbs (Le Boulengé and Fuentes 1978). In addition, degus deposit feces around the entrances of their burrows (Jaksic et al. 1979). Rodent feces are important sources of soil nutrients (Moorhead et al. 1988) and burrow entrances may act as traps for litter burial. This combination results in increasing rates of decomposition and organic matter turnover under shrubs (Steinberger and Whitford 1983), perhaps facilitating the establishment of some annuals such as *M. pinnatifida*, which is restricted to the rich-nutrient areas under bushes (Gutiérrez et al. 1993b). Further research is needed to verify this.

Except for the shrub *C. petiolare*, seed densities all other species responding to the treatments were annuals. For instance, seed densities of *Erodium* spp. (*E. cicutarium*, *E. malacoides*, and *E. moschatum*) were higher in degu-open plots. These species are widespread weeds native to Europe that were probably introduced to Chile by the Spanish (Armesto and Vidiella 1993). Foliage and seeds of *E. cicutarium* have been noted as important food items for degus in central Chile (Meserve 1981a; Meserve et al. 1984) and they are among the main food

items for Sonoran and Chihuahuan desert rodent granivores (Inouye et al. 1980; Samson et al. 1992). Our results suggest that although degus consume *E. cicutarium*, the herbivore effects may be offset by the generation of more favorable microhabitat for weed propagation as a result of degu activity. Positive influences of native small mammals on the renewal of their plant foods have been previously reported for this same ecosystem (Contreras and Gutiérrez 1991; Contreras et al. 1993). Seed densities of *Cuscuta micrantha*, *Descurainia pinnata*, and *Schismus arabicus* were higher in predator-exclusion plots.

These results support the hypothesis that, in general, the presence of degus and the absence of predators do not have detrimental effects on the seed bank or on ephemeral plant cover. Unlike North American deserts, Chilean ones together with the neighboring Argentine Monte Desert have few granivorous rodents, and a greater proportion of herbivorous and insectivorous species (Glanz 1977, 1982, 1984; Mares and Rosenzweig 1977, 1978; Meserve 1981a, b; Morton 1985; Brown and Ojeda 1987; Torres-Mura et al. 1989; Vásquez et al. 1995).

Apparently, degu effects on the plant community are strongly correlated with the availability of plant species in the different localities thus far studied. At Fray Jorge, 2–3 years of drought are quite frequent, thus periodically lowering the biomass of ephemeral plants. On the other hand, shrub cover plus perennial grasses has changed very little over the last 50 years in spite of the high variability and general decline in rainfall during this period (Gutiérrez et al. 1993a). Hence, although shrub tissues contain more complex polysaccharides than herbaceous plants (e.g., cellulose), which are important plant defenses against herbivores, they constitute a more reliable food for degus in this ecosystem. Veloso and Bozinovic (1993) showed that degus have a high physiological and morphological plasticity of the digestive system that allows them to consume plants with different water, fiber, and nutrient concentrations. Another factor that may explain why degus have a greater effect on shrub species instead of the presumably more nutritious ephemeral plants may be related to biological features of this rodent. Typically, at Fray Jorge degus produce a single litter each year, with conception concurrent with the arrival of winter rains (Meserve et al. 1995). Combined with a long gestation period (90 days), and production of large, highly precocious offspring (Woods and Boraker 1975), this results in an intrinsic delay in the adjustment of reproductive rates in response to extrinsic events such as increased plant productivity triggered by high rainfall. Although Rojas et al. (1977) and Zunino and Saiz (1991) emphasized rapid reproductive responses to increased herbage production in central Chile, this is not the case in Fray Jorge. Only by the end of 1992, after the second year of high herbage production, did degu numbers start to increase, reaching maximum numbers in March 1993 (Meserve et al. 1995) at a time when ephemeral plant cover was almost nil. Hence, degu effects due to herbivo-

ry may be protracted. Interestingly, cover of ephemerals by year was always greater in degu-open plots except for 1993. Perhaps this was when direct negative effect of herbivory overrode indirect positive effects of degu activity.

Yearly and seasonal cover and seed bank responses of plant species to degu removal are clearly related to plant growth pulses (i.e., larger differences were observed between degu-open and degu-exclusion plots in wet years and during growing seasons). In low rainfall years (e.g., 1990, 1993, 1994) the role of abiotic factors is greater since plants are limited by rainfall and nutrients; in turn, small mammal numbers are low, and thus, numbers of their predators. In high rainfall years (1991–1992) abiotic factors remain important until populations of consumer organisms and/or their predators become high enough such that they start to exert an effect. Higher cover of some shrubs (e.g., *Proustia pungens* and *Senna cummingii*) and ephemerals (e.g., *A. tenella*) in plots containing predators, suggest a positive indirect effect of predators on plants, presumably by depressing small mammal densities and/or altering their foraging behavior. Indirect effects are generally difficult to detect and usually take place in the long-term (Heske et al. 1994). If indirect effects of either predators or degus are important, we might expect some carryover effects in future years.

Acknowledgements We thank the following people who helped us in various aspects of the field work: W.B. Milstead, B.K. Lang, K.L. Cramer, V.O. Lagos, S.I. Silva, E.L. Tabilo, M.A. Torrealba, A. Levicán, and H. Vásquez. Plant species identification was possible thanks to the invaluable help of G. Arancio (Curator of the Herbarium, Universidad de La Serena). We are grateful to Corporación Nacional Forestal (CONAF) IV Region, and in particular to W. Canto and J. Cerda for permitting the realization of this project in Parque Nacional Fray Jorge. We also appreciate the cooperation of park personnel there. Support for this project has come from the US National Science Foundation (BSR-8806639, DEB-9020047, and DEB-9318565), and Chile's Fondo Nacional de Ciencia y Tecnología (Fondecyt 90-0930 and 193-1150).

References

- Armesto JJ, Vidiella PE (1993) Plant life-forms and biogeographic relations of the flora of Lagunillas (30° S) in the fog-free Pacific coastal desert. *Ann Miss Bot Gard* 80:499–511
- Beatley JC (1974) Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology* 55:856–863
- Brown JH, Heske EJ (1990) Temporal changes in a Chihuahuan Desert rodent community. *Oikos* 59:290–302
- Brown JH, Ojeda RA (1987) Granivory: patterns, processes, and consequences of seed consumption on two continents. *Rev Chil Hist Nat* 60:337–349
- Brown JH, Davidson DW, Munger JC, Inouye RS (1986) Experimental community ecology: the desert granivore system. In: Diamond J, Case TJ (eds) *Community ecology*. Harper and Ross, New York, pp 41–61
- Contreras LC, Gutiérrez JR (1991) Effects of the subterranean herbivorous rodent *Spalacopus cyanus* on the herbaceous vegetation in arid coastal Chile. *Oecologia* 87:106–109
- Contreras LC, Gutiérrez JR, Valverde V, Cox GW (1993) Ecological relevance of subterranean herbivorous rodents in semiarid coastal Chile. *Rev Chil Hist Nat* 66:357–368
- Davidson DW, Samson DA, Inouye RS (1985) Granivory in the Chihuahuan Desert: interactions within and between trophic levels. *Ecology* 66:486–500
- Ende CE von (1993) Repeated measures analysis: growth and other time-dependent measures. In: Scheiner S, Gurevitch J (eds) *The design and analysis of ecological experiments*. Chapman and Hall, New York, pp 113–137
- Fuentes ER, Le Boulengé PY (1977) Predation et compétition dans la dynamique d'une communauté herbacée secondaire du Chili central. *Terre Vie* 31:313–326
- Fuentes ER, Jaksic FM, Simonetti JA (1983) European rabbits versus native rodents in central Chile: effects on shrub seedlings. *Oecologia* 58:411–414
- Fuentes ER, Otaiza RD, Alliende MC, Hoffmann AJ, Poiani A (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* 62:405–411
- Fulk GW (1975) Population ecology of rodents in the semiarid shrublands of Chile. *Occ Pap Mus Texas Tech Univ* 33:1–40
- Fulk GW (1976) Owl predation and rodent mortality: a case study. *Mammalia* 40:423–427
- Glanz WE (1977) Comparative ecology of small mammal communities in California and Chile. Ph D dissertation University of California, Berkeley
- Glanz WE (1982) Adaptive zones of Neotropical mammals: a comparison of some temperate and tropical patterns. In: Mares MA, Genoways HH (eds) *Mammalian biology in South America* (Special Publications, Pymatuning Laboratory of Ecology). University of Pittsburg, Linesville, Pennsylvania, pp 95–110
- Glanz WE (1984) Ecological relationships of two species of *Akodon* in central Chile. *J Mammal* 65:433–441
- Gutiérrez JR, Meserve PL, Jaksic FM, Contreras LC, Herrera S, Vásquez H (1993a) Structure and dynamics of vegetation in a Chilean arid thorn scrub community. *Acta Oecol* 14:271–285
- Gutiérrez JR, Meserve PL, Contreras LC, H. Vásquez, Jaksic FM (1993b) Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* (Zygophyllaceae) shrubs in arid coastal Chile. *Oecologia* 95:345–352
- Heske EJ, Brown JH, Guo Q (1993) Effect of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95:520–524
- Heske EJ, Brown JH, Mistry S (1994) Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75:438–445
- Huntley N, R. Inouye R (1988) Pocket gophers in ecosystems: patterns and mechanisms. *BioScience* 38:786–793
- Inouye RS, Byers GS, Brown JH (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61:1344–1351
- Jaksic FM (1986) Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences. *Rev Chil Hist Nat* 59:209–221
- Jaksic FM, Fuentes ER (1980) Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing? *J Ecol* 68:665–669
- Jaksic FM, Fuentes ER, Yañez JL (1979) Spatial distribution of the Old World rabbit (*Oryctolagus cuniculus*) in central Chile. *J Mammal* 60:207–209
- Jaksic FM, Greene HW, Yañez JL (1981) The guild structure of a community of predatory vertebrate in central Chile. *Oecologia* 49:21–28
- Jaksic FM, Jiménez JE, Castro SA, Feinsinger P (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. *Oecologia* 89:90–101
- Jaksic FM, Meserve PL, Gutiérrez JR, Tabilo E (1993) The components of predation on small mammals in semiarid Chile: preliminary results. *Rev Chil Hist Nat* 66:305–321
- Lagos VO, Contreras LC, Meserve PL, Gutiérrez JR, Jaksic FM (1995) Predation effects on space use by small mammals: a field experiment with a Neotropical rodent. *Oikos* 74:259–264
- Le Boulengé E, Fuentes ER (1978) Quelques données sur la dynamique de population chez *Octodon degus* (Rongeur Hystricomorphe) due Chili central. *Terre Vie* 32:325–341

- Ludwig JA, Whitford WG (1981) Short-term water and energy flow in arid ecosystems. In: Goodall DW, Perry RA (eds) *Arid-land ecosystems: structure, functioning and management*. Cambridge University Press, Cambridge, pp 271–299
- Mares MA, Rosenzweig ML (1977) Seeds-seed eater system. In: Orians GH, Solbrig OT (eds) *Convergent evolution in warm deserts*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp 196–204
- Mares MA, Rosenzweig ML (1978) Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* 59:235–241
- Martinsen GD, Cushman JH, Whitham TG (1990) Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. *Oecologia* 83:132–138
- Meserve PL (1981a) Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. *J Mammal* 62:304–314
- Meserve PL (1981b) Resource partitioning in a Chilean semiarid small mammal community. *J Anim Ecol* 50:745–757
- Meserve PL, Martin RE, Rodríguez J (1984) Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean mediterranean-type communities. *Rev Chil Hist Nat* 57:79–89
- Meserve PL, Gutiérrez JR, Jaksic FM (1993a) Effects of vertebrate predation on a caviomorph rodent, the degu (*Octodon degus*), in a semiarid thorn scrub community in Chile. *Oecologia* 94:153–158
- Meserve PL, Gutiérrez JR, Contreras LC, Jaksic FM (1993b) Role of biotic interactions in a semiarid scrub community in north-central Chile: a long-term ecological experiment. *Rev Chil Hist Nat* 66:224–241
- Meserve PL, Yungler JA, Gutiérrez JR, Contreras LC, Milstead WB, Lang BK, Cramer KL, Herrera S, Lagos VO, Silva SI, Tabilo EL, Torrealba MA, Jaksic FM (1995) Heterogeneous responses of small mammals to an El Niño (ENSO) event in north-central semiarid Chile and the importance of ecological scale. *J Mammal* 76:580–595
- Meserve PL, Gutiérrez JR, Yungler JA, Contreras LC, Jaksic FM (1996) Role of biotic interactions in a small mammal assemblage in semiarid Chile. *Ecology* 77:133–148
- Moorhead DL, Fisher FM, Whitford WG (1988) Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan Desert grassland. *Am Midl Nat* 120:44–447
- Morton SR (1985) Granivory in arid regions: comparison of Australia with North and South America. *Ecology* 66:1859–1866
- Mueller-Dombois D, Ellenberg H (1974) *Aims and methods of vegetation ecology*. Wiley, New York
- Muñoz C, Pisano E (1947) Estudio de la vegetación y flora de los parques nacionales de Fray Jorge y Talinay. *Agr Téc Chile* 2:71–190
- Noy-Meir I (1973) Desert ecosystems: environments and producers. *Ann Rev Ecol Syst* 4:25–51
- Reichman OJ (1984) Spatial and temporal variation of seed distributions in Sonoran Desert soils. *J Biogeogr* 11:1–11
- Rojas M, Rivera O, Montenegro G, Barros C (1977) Algunas observaciones en la reproducción de la hembra silvestre de *Octodon degus* Molina y su posible relación con la fenología de la vegetación. *Medio Ambient Chile* 3:78–82
- Samson DA, Philippi TE, Davidson DW (1992) Granivory and competition as determinants of annual plant diversity in the Chihuahuan Desert. *Oikos* 65:61–80
- SAS (1988) SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary
- Scheiner SM (1993) MANOVA: Multiple response variables and multispecies interactions. In: Scheiner SM, Gurevitch J (eds) *The design and analysis of ecological experiments*. Chapman and Hall, New York, pp 94–112
- Simonetti JA, Montenegro G (1981) Food preferences by *Octodon degus* (Rodent: Caviomorpha): their role in the Chilean matorral composition. *Oecologia* 51:189–190
- Steinberger Y, Whitford WG (1983) The contribution of rodents to decomposition processes in a desert ecosystem. *J Arid Environ* 6:177–181
- Swihart RK (1991) Influence of *Marmota monax* on vegetation in hayfields. *J Mammal* 72:791–795
- Torres-Mura JC, Lemus ML, Contreras LC (1989) Herbivorous specialization of the South American desert rodent *Tympanotomys barrerae*. *J Mammal* 70:646–648
- Vásquez RA, Bustamante RO, Simonetti JA (1995) Granivory in the Chilean matorral: extending the information on arid zones of South America. *Ecography* 18:403–409
- Veloso C, Bozinovic F (1993) Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. *Ecology* 74:2003–2010
- Whickler AD, Detling JK (1988) Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785
- Whitford WG (1993) Animal feedbacks in desertification: an overview. *Rev Chil Hist Nat* 66:243–251
- Whittaker RH (1975) *Communities and ecosystems*, 2nd edn. MacMillan, New York
- Woods CA, Boraker DK (1975) *Octodon degus*. *Mammal Spec* 67:1–5
- Zunino S, Saiz F (1991) Estructura y densidad poblacional de *Octodon degus* Mol. *Stud Neotropical Fauna Environ* 26:143–148