

Ecology, 77(1), 1996, pp. 133–148
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**ROLE OF BIOTIC INTERACTIONS IN A SMALL MAMMAL
ASSEMBLAGE IN SEMIARID CHILE¹**

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Abstract. The role of biotic interactions including vertebrate predation and interspecific competition was studied among members of a semiarid small mammal assemblage in a long-term field manipulation in north central Chile. Fences and netting selectively excluded mammalian and avian predators, and a putative rodent competitor, the degu (*Octodon degus*), from large, replicated grids. Small mammal populations were censused monthly over >4 yr, and effects of predator and degu exclusions on numbers and survival of small mammals were assessed with repeated measures ANOVAs. Marginally significant predator exclusion effects were detected on *O. degus*, and highly significant year × predation interactions in both wet and dry seasons; degu survival (= persistence) was also significantly longer on exclusion grids. Predation had significant effects on numbers of *Phyllotis darwini*, and a significant month × predator interaction existed in the wet season; survival was also significantly higher on predator exclusion grids. There was a marginally significant year × competitor interaction in the dry season for this species. *Akodon olivaceus* had significant month × predator and month × competitor interactions in the wet season only; survival was significantly longer on degu exclusion grids. An irruptive species, *Oligoryzomys longicaudatus*, showed no significant predator or competitor effects in 1991–1992; however, survival was significantly longer on predator + competitor exclusion (vs. control) grids. An uncommon species, *Abrothrix longipilis*, had marginally nonsignificant time × competitor interactions but no treatment differences in survival. Finally, a second uncommon rodent, *Abrocoma bennetti* (not analyzed numerically) had significantly longer survival on predator exclusion grids with degus. Degus and *P. darwini* were significantly overrepresented (relative to availability) in diets of culpeo foxes (*Pseudalopex culpaeus*) and three nocturnal owls, respectively, whereas *A. bennetti* was significantly overrepresented in predator diets generally. Vertebrate predation has pervasive effects on some species that, however, may be related to their intrinsic demographic characteristics. Competition may be mediated by subtle behavioral interactions among assemblage members. Long-term studies are necessary to elucidate the role of biotic and abiotic factors in semiarid environments.

Key words: Chile; competition; ecological scale; semiarid zone; small mammals; South America; vertebrate predation.

INTRODUCTION

Much attention has been focused on the importance of biotic interactions in community ecology. Observational and comparative approaches have been most often utilized in field studies of such interactions (Krebs 1988, Hom and Cochran 1991). These made up 76% of the ecological studies surveyed by Tilman (1989); Hom and Cochran (1991) found a similar figure

(67.2%) for observational studies of birds and mammals. Once the natural history of a particular group of organisms is sufficiently well known, a manipulative approach may be the only way to understand the role of biotic factors in the community.

Higher vertebrate organisms are poorly represented in field studies of biotic interactions in the literature. Schoener (1983) and Connell (1983) cited only 29 (out of 164; 17.9%) and 11 (out of 72; 15.3%) experimental studies, respectively, of interspecific competition involving birds and mammals. Dueser et al. (1989) reviewed 25 experimental studies of competition in ro-

¹ Manuscript received 27 June 1994; revised 3 March 1995; accepted 18 March 1995; final version received 21 April 1995.

dents, and frequently noted low replication (or pseudoreplication sensu Hurlburt [1984]) as well as high within-treatment variation. Experimental studies of predation are similarly underrepresented among vertebrates (re Kerfoot and Sih 1987); only 19 of 139 predation studies (13.7%) listed by Sih et al. (1985) involved birds and/or mammals.

A further consideration has been the problem of ecological scale (e.g., Wiens 1986, 1989, Wiens et al. 1986, Giller and Gee 1987, O'Neill 1988, Powell 1989, Steele 1989, Levin 1992). The majority of ecological studies occur on a short temporal scale; Tilman (1989) found that 86% of 180 manipulative field experiments published in *Ecology* in 1977–1987 lasted 3 yr/field seasons or less; only 7% had a duration of 5 yr/field seasons or more. Long-term studies provide opportunities to examine ecological processes at various temporal scales (Likens 1989, Risser 1991). Without such data, it is difficult to assess the significance of changes in numbers and periodicity of organisms that may experience long-interval oscillations. More generally, the issue is not whether any one scale in space or time is "correct," but rather understanding exactly what is being measured at a particular scale in studying ecological phenomena (Levin 1992).

Only a few studies have applied field manipulations to small mammals on a relatively long time scale (e.g., Munger and Brown 1981, Brown and Munger 1985, Brown et al. 1986, Brown and Heske 1990, Heske et al. 1994, Valone and Brown 1995). These studies and those of Brown et al. (1979a, b) and Davidson et al. (1980, 1984, 1985) have emphasized interactions between granivorous rodents and other seed-eating groups such as ants and birds as well as direct and indirect interactions with plants in the community. Other studies have emphasized the role of biotic interactions on shorter time scales (e.g., Grant 1969, 1972, Krebs et al. 1969). The problem of spatial scale is equally important (Wiens 1986, 1989, Wiens et al. 1986). Half of nearly 100 field experiments surveyed by Kareiva and Andersen (1988, as cited in Wiens 1989) were done on plots $\leq 1 \text{ m}^2$. Selection of the appropriate spatial scale is a function of both areal extent and individual observation unit or grain (sensu O'Neill et al. 1986, Wiens 1989).

The Chilean mediterranean-type region received considerable attention due to the major focus of the International Biological Program (1967–1974) on convergent properties with mediterranean regions in California and elsewhere. Results of this work (summarized in di Castri and Mooney 1973, Cody et al. 1977, Mooney 1977, Mooney et al. 1977, Thrower and Bradbury 1977) suggested that between-habitat (β) small mammal diversities were conspicuously lower in Chile than in California while α (within-habitat) diversities were similar. Species tended to occur in many habitats in Chile, with little reciprocal replacement by ecologically similar forms in different habitats. Chilean small

mammals also demonstrated strong selection for areas of high shrub cover and high habitat overlap (Glanz 1977, Meserve 1981a, Glanz and Meserve 1982). Mediterranean Chile has a diverse predator assemblage of raptors, mammalian carnivores, and reptiles (Jaksic et al. 1981) for which small mammals are important prey (Jaksic et al. 1981, 1993, Jaksic 1986). This suggests a major role of predation in this region (e.g., Jaksic et al. 1979, 1981, Jaksic 1986, Simonetti 1989a, b). Chilean small mammals have about the same dietary overlap as do those in mediterranean California (Meserve 1981a) but have more clearly defined trophic niches (Meserve 1981b). In the central Chilean mediterranean zone as well as northern semiarid fringe, only two species are usually present in each trophic category (except for one omnivore). The second species is conspicuously less abundant (Glanz 1977, 1982, 1984, Meserve 1981a, b, Glanz and Meserve 1982, Meserve et al. 1983), whereas California mediterranean scrub communities have more equitable numbers of two or more small mammal species in similar trophic categories including omnivores (Meserve 1976a, b, Glanz 1977). The role of interspecific competition is poorly known, however, particularly in the Chilean assemblage, and there have been few experimental studies of predation or competition generally in the temperate (or tropical) Neotropics (e.g., August and Fleming 1984, Simonetti et al. 1985, Murúa et al. 1987).

We have been conducting a long-term manipulation at a semiarid study site in north central Chile since 1989. The objective has been to quantify the role of biotic interactions in small mammal and plant assemblages, as well as the importance of large scale abiotic events such as El Niño Southern Oscillations (ENSO). We utilized a multifactorial approach since simultaneous biotic interactions including predation, competition, and herbivory may play an interactive role (Lubchenco 1986, Roughgarden and Diamond 1986, Lidicker 1991).

MATERIALS AND METHODS

The study area is located in Parque Nacional Fray Jorge (71°40' W, 30°38' S; IV [Coquimbo] Region) $\approx 100 \text{ km}$ south of La Serena and 350 km north of Santiago, Chile near the coast (Fig. 1). This 10 000-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 well-known flora of the lower elevational scrub zone (Muñoz and Pisano 1947, Muñoz 1985, Hoffmann 1989, Gutiérrez et al. 1993a) includes spiny drought-deciduous and evergreen shrubs and understory herbs on a predominantly sandy substrate, and is termed the *Porlieria chilensis*–*Proustia pungens*–*Adesmia bedwellii* association (Muñoz and Pisano 1947). The climate is semiarid mediterranean with 90% of the mean 85 mm annual precipitation falling in winter months (May–October); summer months are warm and

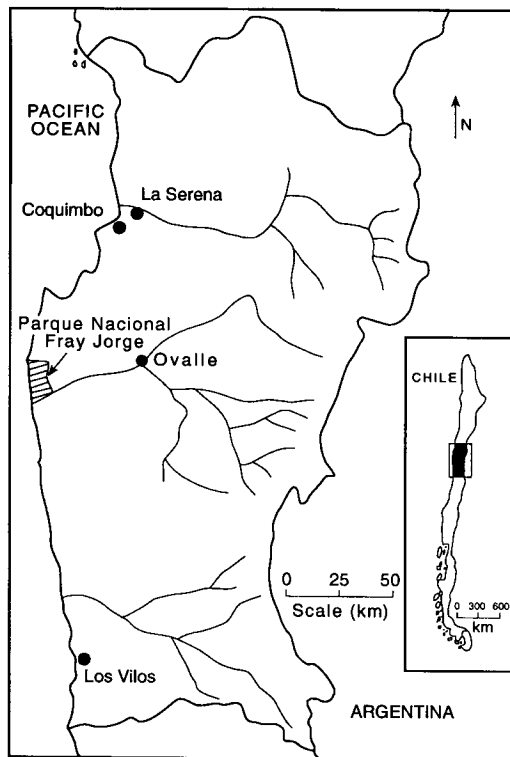


FIG. 1. Location of Parque Nacional Fray Jorge in the IV Region (Coquimbo) in north central Chile. Major river courses and cities are also indicated.

dry. During 1991–1992, an ENSO event was in progress. 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).

The principal study area ("Quebrada de las Vacas," 240 m elevation) has a homogeneous community of thorn scrub and was the focus of work by Fulk (1975, 1976), Meserve (1981a, b) and Meserve and Le Boulengé (1987). In addition to the previously noted small mammals, the important vertebrate predators include owls (*Speotyto cunicularia*, *Tyto alba*, *Bubo virginianus*, and *Glaucidium nanum* [sporadic]) and the culpeo fox (*Pseudalopex culpaeus*); small mammals are major prey for most of them (Fulk 1976, Jaksic et al. 1981, 1992, 1993, Meserve et al. 1987). Predator concentrations within park boundaries are particularly high since it has one of the only significant areas of undisturbed semiarid scrub in north central Chile.

Following initial surveys in late 1988, 16, 75 × 75 m (0.56 ha) grids were delineated in the valley in January–March 1989, and monthly small mammal trapping initiated. Since March 1989, live-trap small mammal censuses have been conducted for four nights per month on each of the 16 grids (5 × 5 stations, two traps per station, 15-m interval). Animals are marked with ear tags or leg bands, and data taken on tag num-

ber, species, sex, mass, reproductive condition, and capture location during handling. Data are analyzed with the capture–mark–recapture (CMR) programs of Le Boulengé (1985; example of application in Meserve and Le Boulengé 1987).

Year-round members of the small mammal assemblage included the caviomorph rodent *Octodon degus* (degu) and the sigmodontine rodents *Akodon olivaceus* (olivaceous field mouse) and *Phyllotis darwini* (leaf-eared mouse). Other species such as *Oligoryzomys longicaudatus* (long-tailed rice rat), *Abrothrix longipilis* (long-haired field mouse), *Thylamys (Marmosa) elegans* (mouse opossum; Marmosidae, Didelphoidea), and *Abrocoma bennetti* (chinchilla rat; Abrocomidae, Rodentia) were sporadic and/or uncommon in occurrence (Meserve and Le Boulengé 1987). Monthly trappabilities (percentage of censuses in which known resident individuals were caught at least once) for the principal species (except *O. degus*) and *O. longicaudatus* exceeded 90% through 52 monthly censuses. Thus, we utilized minimum number known alive (MNKA) estimates per grid for analyses of population trends. The first five species noted above were considered separately in analyses. Other species were considered only qualitatively except for survival analysis of *A. bennetti*.

The description of the experimental design is as follows (see also Meserve et al. 1993a):

(1) four 0.56-ha grids have low (1.0 m high) fencing buried ≈ 40 cm into the ground with enlargements of the 2.5-cm mesh cut in the chicken wire (yielding ≈ 5 cm diameter holes) at ground level to allow all small mammal and predator access (hereafter referred to as controls or +D +P grids);

(2) four grids have high (1.8 m high) fencing buried 40 cm, a 1 m high overhang, polyethylene netting (≈ 15 cm diameter mesh) overhead, and holes in the fencing to exclude predators but allow small mammal access (including degus; +D –P grids);

(3) four grids have low (1.0 m high) fencing buried 40 cm without holes to exclude the principal small mammal herbivore (and here, putative competitor), the degu (*O. degus*) but not other small mammals or predators (–D +P grids); and

(4) four grids have high (1.8 m high) fencing buried 40 cm with overhangs and netting but without holes in the fencing to exclude both predators and degus (–D –P grids).

For statistical analysis, the experiment is a 2 × 2 factorial design with treatments being competition (presence or absence) and predation (presence or absence). Treatments were randomly assigned. Both single and doubly within-subject repeated measures analysis of variance (rmANOVA; PROC ANOVA, SAS 1990a) were used to analyze MNKA estimates of small mammal numbers by season (Potvin et al. 1990, von Ende 1993). Between-subject factors were predation (for degus) and predation and competition (for non-

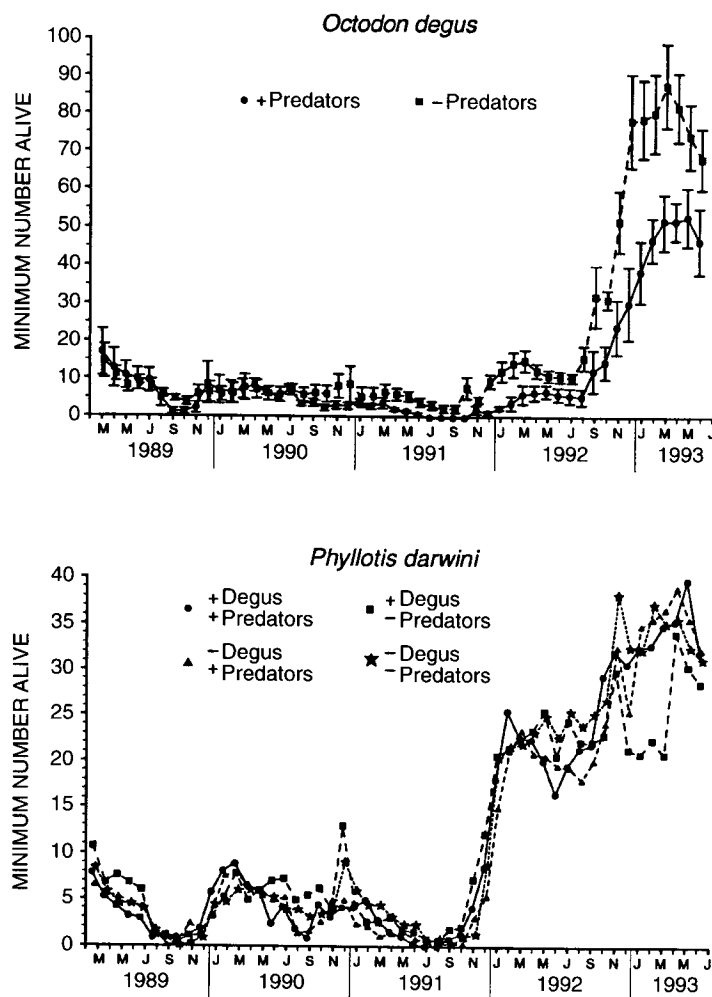


FIG. 2. Population trends of *Octodon degus* and *Phyllotis darwini* during March 1989 through June 1993. Treatments indicated by symbols and adjacent labels; one standard error of the mean indicated for *O. degus* only.

degus); within-treatment factors were year and month. Between- and within-subject interactions were also examined. The within-subject year and month terms were discussed in Meserve et al. (1995); an α of $P \leq 0.05$ was used. Data were analyzed from censuses for 6-mo periods over 4 yr distinguishing the cooler wet season (May–October) and warmer dry season (November–April). This procedure avoided confounding treatment effects with seasonal patterns of reproduction, recruitment, and declines typical of small mammals at this locality (Meserve 1981a, Meserve and Le Boulengé 1987, Meserve et al. 1995). Statistical inferences were based on Type III sum-of-squares and all P values for within-subject analyses were Huynh-Feldt adjusted, which corrects for deviations in the sphericity assumption of the variance–covariance matrix (von Ende 1993). Since an assumption of ANOVA is homogeneity of variances, an F_{\max} test (Sokal and Rohlf 1981), which has a high Type I error rate (Conover et al. 1981), was used to evaluate evidence for heteroscedasticity of between-subject cell variances. Only one out of eight rmANOVAs (that for *A. olivaceus* during the wet sea-

son) showed such evidence; however, the minimum-to-maximum variance ratio was within acceptable limits for satisfying the assumptions of ANOVA, which is robust for such deviations (Maxwell and Delaney 1990). The distribution of the residuals was inspected with Tukey box-plots and log–log probability plots. In all instances, the residuals approximated a normal distribution and no transformations were performed.

Survival rates were analyzed for adult and subadult individuals (defined in Meserve and Le Boulengé 1987, Meserve et al. 1995) of the principal species for the entire period (May 1989 through April 1993) with PROC LIFETEST (SAS 1990b). Individuals surviving from prior to the initiation of the experiment in May 1989 (i.e., left-censored observations) were included in the analysis, as were those surviving past the end of the analysis period (i.e., April 1993), which were right-censored observations (see Lee 1980). Individuals from all four grids in a treatment were pooled to increase sample size. Statistical comparisons of overall survival were conducted with the nonparametric log-rank test, which is robust to differences in survival

TABLE 1. Results of doubly within-subject repeated measures ANOVA of minimum number known alive per grid for *Octodon degus* during the wet season and dry season. Within-subject *P* values are Huyhn-Feldt adjusted.

Source of variation	df	Wet season			Dry season		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Between subject							
Predation	1	663.80	3.82	0.098	7093.17	5.19	0.051
Error	6	173.76			1199.98		
Within subject							
Year	3	1045.71	25.55	<0.001	29224.06	81.22	<0.001
Year × predation	3	210.06	5.12	0.010	7971.35	7.38	0.006
Error (year)	18	41.00			359.82		
Month	5	35.72	6.17	0.015	196.93	3.86	0.053
Month × predation	5	61.76	10.66	0.002	44.03	0.86	0.443
Error (month)	30	5.79			50.97		
Year × month	15	142.81	19.19	<0.001	353.82	5.22	0.027
Year × month × predation	15	16.42	2.21	0.101	106.55	1.57	0.250
Error (year × month)	90	7.44			67.74		

curve shape and does not assume any particular underlying distribution (Lee 1980, Fox 1993). Multiple comparisons were performed for species with an overall significant survival effect. Since no specific a posteriori tests are available for comparison of multiple survival curves, single probability *z* scores were calculated using the covariance matrix generated by PROC LIFETEST. *P* values were then calculated based on the *z* scores and significance determined from Bonferroni-adjusted α 's (Winer et al. 1991). Only uncensored observations were plotted for graphical representations of survivorship. Predator scat and pellet data were analyzed for the same periods using χ^2 goodness-of-fit tests comparing observed frequencies of prey in predator diets and trap-revealed numbers on control (+D +P) grids, and preliminary results have been reported elsewhere (Jaksic et al. 1993). Since fence construction was not completed until late May 1989, and degu removals were initiated after then, the first 3 mo (March–May) constituted a pretest period.

RESULTS

Through November 1991, 11 551 captures (10.9% trap success) of 2720 individuals of eight species were recorded. Numbers of captures per month then increased almost two orders of magnitude during 1992 and reached ≈ 4600 per month with almost 100% trap success in mid-1993; 81 212 captures were recorded through June 1993. The responses of small mammals to the 1991–1992 ENSO are reported elsewhere (Meserve et al. 1995), as are the plant responses to degu and/or predator exclusions (Gutiérrez et al. 1993b and unpublished data).

During the pretest period (March–May 1989), there were no significant differences observed between treatments with respect to densities of principal species (*Octodon degus*: rmANOVAs, $F_{1,6} = 0.23$, $P = 0.65$; other principal species: all $F_{1,12} \leq 2.36$, all $P \geq 0.15$). Supplemental diurnal trapping outside fenced grids in August 1992 revealed that numbers of degu were lower

in open areas than in fenced control (i.e., +D +P) and predator exclusion grids (+D –P). This suggests that the use of fences in degu access grids (+D) did not adversely influence their densities. In fact, control grids may have had slightly greater numbers, which rendered comparisons with predator exclusion grids (i.e., +D –P) conservative. Numbers of degu inside exclusion grids (i.e., –D +P, –D –P) after removal initiation in June 1989 ranged from 0 to 5 per grid per month until December 1992–January 1993 when they increased to a maximum of 20–30 per grid; these subsequently declined. Since removals were conducted monthly, these probably represent peak levels, and the degu exclusions could be considered reasonably effective over most of the study period. The large increase in degu populations generally in response to the 1991–1992 ENSO was responsible for decreased effectiveness of exclusions especially in –D +P grids with low fencing.

Initial results of predator exclusions on *O. degus* through 1991 were reported elsewhere (Meserve et al. 1993b). One-way MANOVAs for 3-mo periods showed strongest but nonsignificant effects of predator exclusions during spring months (September–November) of 1989 and 1990; in September–November 1991 treatment effects were significant ($F_{1,6} = 10.52$, $P = 0.016$; Fig. 2). Repeated measures ANOVAs showed marginally significant between-subject effects during the dry season (Table 1). There were also highly significant year × predator interactions during both wet and dry seasons, and month × predator interactions during the wet season (Table 1). Plots of these interactions showed that predation effects on *O. degus* diverged over time in both seasons (Fig. 3A, B) as did month × predator effects over all years (Fig. 3C). Effects became more pervasive during high degu population levels in 1992 and 1993 (Fig. 2). Therefore, predation had significant effects on this species and became amplified at higher densities. Degu experienced a delayed response to the 1991–1992 ENSO increasing to maximum levels only during 1992 and 1993 (Meserve et al. 1995; Fig. 2).

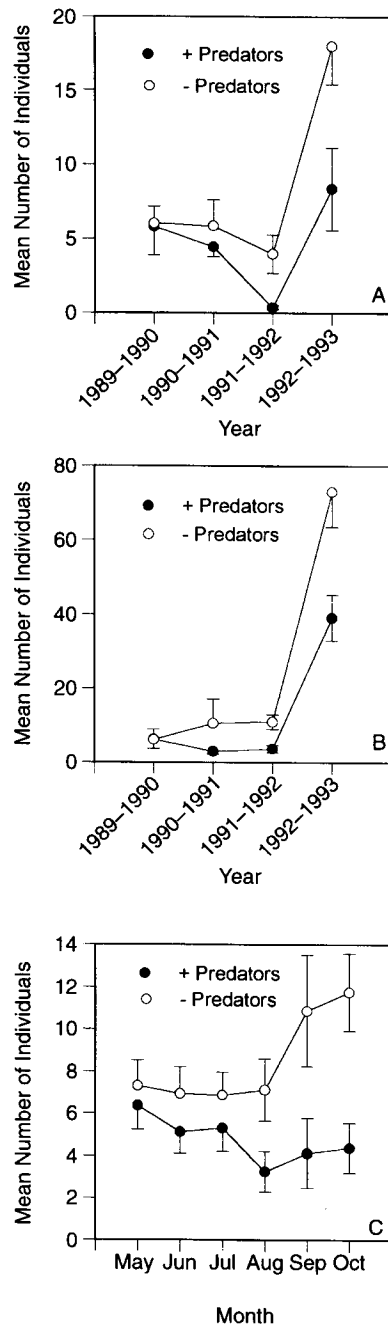


FIG. 3. Mean numbers of degus (*Octodon degus*)/grid \pm 1 standard error during (A) wet season months (May–October) by year (1989–1993), (B) dry season months (November–April) by year (1989–1993), and (C) wet season (May–October) by month on predator open (+predators) and predator exclusion (–predators) grids.

Degu survivorship was significantly greater on predator exclusion grids than controls (Fig. 4A; log-rank test, $\chi^2 = 13.25$, $P < 0.001$). Only 7 of 545 individuals survived >17 mo on predator open grids (maximum = 46 mo); in contrast, 19 of 708 individuals survived

>17 mo on predator exclusion grids (maximum = 46 mo).

Responses of the other principal small mammal species to predator exclusions revealed the interaction of biotic and abiotic factors in this assemblage (Meserve et al. 1995). *Phyllotis darwini* had the most consistent changes in population numbers reflecting annual patterns of reproduction and recruitment (Fig. 2). There was a highly significant between-subject effect of predation on this species during the wet season (Table 2). Within-subject rmANOVAs for wet and dry season months also showed a significant month \times predator effect on this species in the dry season (Table 2). Plots of the densities within the wet season show that *P. darwini* densities were consistently higher on predator exclusion grids both by month and overall (Fig. 5A, B). During the dry season, population trends reversed showing a significant interaction (Fig. 5C). These may reflect transitional effects of predation mixed with demographic changes as significant recruitment occurred into the trappable population (Meserve et al. 1995). There was also a marginally significant year \times competitor interaction during the dry season across all years (Table 2; Fig. 5D).

There was a significant treatment effect on *P. darwini* survival ($\chi^2 = 15.94$, $P = 0.001$). Multiple comparisons showed that significant differences in survivorship existed for this species between +D +P and –D –P treatments and between –D +P and –D –P treatments; the difference between +D –P and –D –P treatments was marginally nonsignificant (Table 3; Fig. 4B). Therefore, while competition with degus had some effect on *P. darwini*, particularly in the dry season over years, predation had the strongest overall effects on both numbers and survival.

The responses of *Akodon olivaceus* illustrated the importance of abiotic factors. Prior to late 1991, numbers of *A. olivaceus* were ≤ 9 individuals per grid (Fig. 6); thereafter, numbers increased to 60–65 individuals per grid in early 1992, and even higher densities in December 1992–January 1993. This species had the most dramatic response to ENSO events at this site increasing rapidly towards the end of the wet season (October–November; Meserve et al. 1995). There were no significant between-subject effects of predation or competition on this species in either season (Table 4). However, there was a significant month \times predator and month \times competitor interaction during the wet season for this species, and a marginally significant month \times competitor interaction during the dry season. Plots of monthly trends indicated that *A. olivaceus* densities reversed between predator exclusion and predator open grids (Fig. 7A) leading to a significant interaction. However, on degu (competitor) exclusion grids, numbers of *A. olivaceus* were higher in 5 of 6 mo of the wet season, and 4 of 6 mo of the dry season across all 4 yr (Fig. 7B, C).

Survival of *A. olivaceus* was significantly different

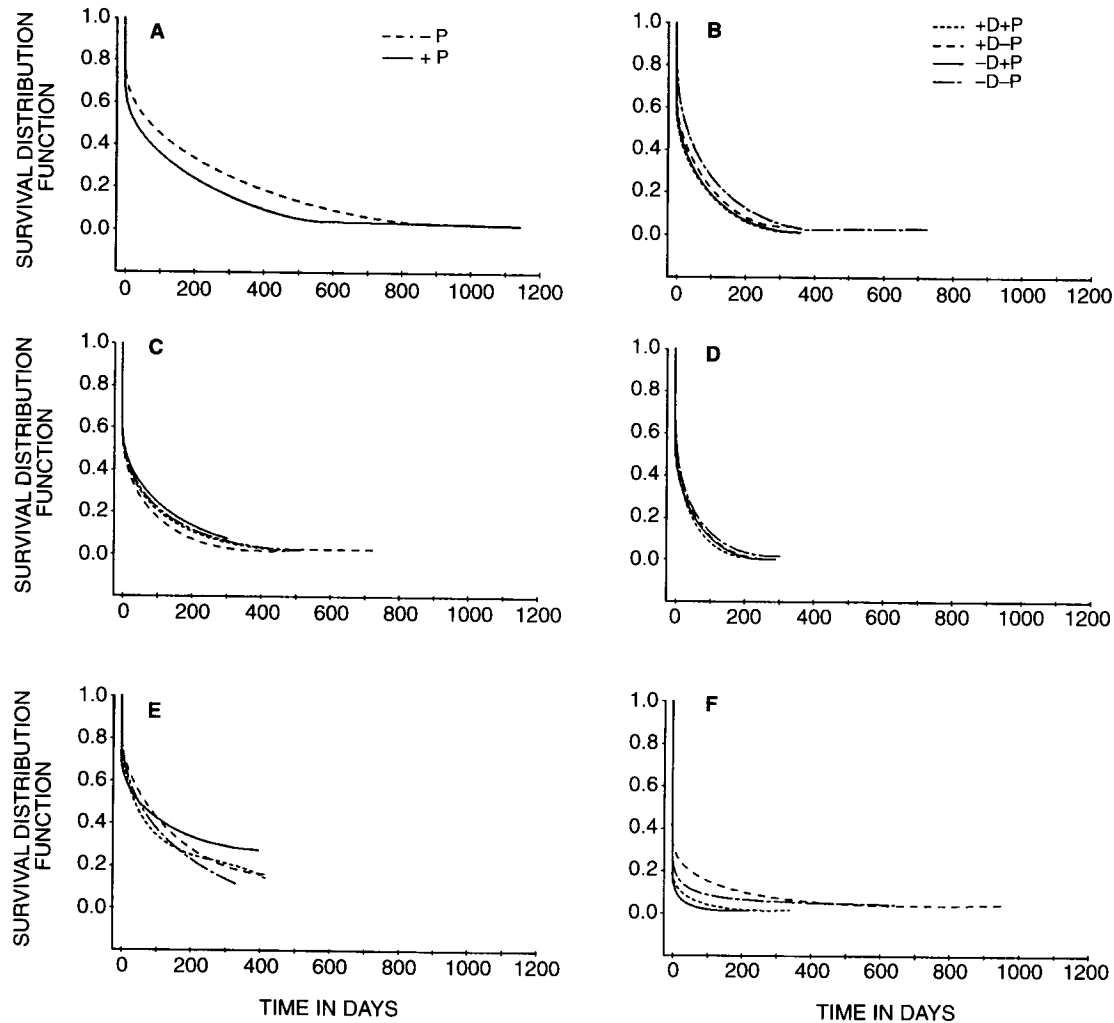


FIG. 4. Survival rates (uncensored observations only; see *Materials and methods*) during May 1989–April 1993 for (A) *Octodon degus* on predator open (+P) and predator exclusion (–P) grids, and (B) *Phyllotis darwini*, (C) *Akodon olivaceus*, (D) *Oligoryzomys longicaudatus*, (E) *Abrothrix longipilis*, and (F) *Abrocoma bennetti* on degu + predator open (+D +P), predator exclusion (+D –P), degu exclusion (–D +P), and degu + predator exclusion (–D –P) grids.

overall among treatments ($\chi^2 = 8.70$, $P = 0.034$). Multiple comparisons revealed that survivorship was significantly different between +D –P and –D –P treatments (Table 3; Fig. 4C). Therefore, unlike *P. darwini*, *A. olivaceus* appeared to be more strongly affected by competitive interactions with *O. degus* than by predation. Overall, this species demonstrated the greatest competitive effects of degus on both its numbers and survivorship.

Trends for *Oligoryzomys longicaudatus* showed two oscillations, one in a dry year (1990), and one in a wet year (1992; Fig. 6). Due to the irruptive nature of their populations and low numbers in most months, data were analyzed as a continuous time series for the period of October 1991–November 1992. There were no significant between-subject or within-subject effects for this species (Table 5). Survival, however, did differ significantly overall ($\chi^2 = 8.36$, $P = 0.039$). Multiple

comparisons of survivorship revealed that significant differences were present between +D +P and –D –P treatments (Table 3; Fig. 4D).

Patterns in a second sigmodontine, *Abrothrix longipilis* were analyzed also as a continuous time series for the last 18 mo of the study (i.e., November 1991–April 1993) since it became uncommon prior to the 1991–1992 ENSO. Cumulative population trends for this and those of two other uncommon species (*Abrocoma bennetti* and *Thylamys elegans*) were intermediate to those of *P. darwini* and *O. degus* with, however, considerably more monthly fluctuation (Fig. 6). Although no significant predator or competitor effects were detected on this species for between-subject analysis, a marginally nonsignificant time \times competitor effect was suggestive of effects of *O. degus* similar to those on *A. olivaceus* (Table 5). Overall survival was not, however, significantly different on predator or

TABLE 2. Results of doubly within-subject repeated measures ANOVA of minimum number known alive per grid for *Phyllotis darwini* during the wet season and dry season. Within-subject *P* values are Huyhn-Feldt adjusted.

Source of variation	df	Wet season			Dry season		
		MS	F	P	MS	F	P
Between subject							
Predation	1	258.30	13.29	0.003	10.34	0.12	0.732
Competition	1	8.46	0.44	0.522	54.75	0.65	0.435
Predation × competition	1	0.44	0.02	0.883	185.65	2.21	0.163
Error	12	19.44			83.82		
Within subject							
Year	3	8977.80	539.82	<0.001	15189.85	202.60	<0.001
Year × predation	3	28.77	1.73	0.197	150.50	2.01	0.159
Year × competition	3	4.09	0.25	0.794	253.05	3.38	0.054
Year × predation × competition	3	32.84	1.97	0.158	103.11	1.38	0.272
Error (year)	36	16.63			74.98		
Month	5	49.00	10.26	<0.001	413.48	39.67	<0.001
Month × predation	5	10.16	2.13	0.081	40.92	3.93	0.010
Month × competition	5	5.38	1.13	0.356	10.39	1.00	0.414
Month × predation × competition	5	10.87	2.28	0.064	19.24	1.85	0.143
Error (month)	60	4.78			10.42		
Year × month	15	37.20	8.96	<0.001	290.23	29.45	<0.001
Year × month × predation	15	8.21	1.98	0.056	17.84	1.81	0.040
Year × month × competition	15	2.21	0.53	0.832	9.46	0.96	0.497
Year × month × predation × competition	15	3.48	0.84	0.572	14.58	1.48	0.123
Error (year × month)	180	4.15			9.86		

competitor exclusion grids ($\chi^2 = 3.91$, $P = 0.272$; Fig. 4E).

Population trends of *A. benetti* and *T. elegans* were not analyzed with rmANOVA due to low numbers, low monthly trappability, and considerable movement between grids. However, overall survival of *A. benetti* was significantly different ($\chi^2 = 11.85$, $P = 0.008$; Fig. 4F) whereas that of *T. elegans* showed no difference ($\chi^2 = 4.161$, $P = 0.245$). Multiple comparisons (Table 3) showed that *A. benetti* had significantly longer survival on +D -P vs. -D +P treatments; the difference between +D +P and +D -P grids was marginally nonsignificant. An eighth species, the coastal degu (*Octodon lunatus*) was recorded in only 2/52 mo (three individuals) through May 1993.

E. M. Jaksic et al. (1993; unpublished data) summarized preliminary results from dietary analysis of scats and pellets of the five predators noted previously. The owls *Speotyto cunicularia*, *Bubo virginianus*, and *Tyto alba* behaved similarly, selecting the nocturnal *A. benetti* and *P. darwini* and underconsuming the remaining five species (except for *B. virginianus*, which also selected the diurnal *O. degus*; Jaksic et al. 1993). A fourth owl, *G. nanum*, was mostly insectivorous until 1992 when small mammals were an important proportion of its diet. Foxes preferred *A. benetti* but also the diurnal *O. degus* (Jaksic et al. 1993). Thus, it appears that only *A. benetti* was a "preferred" prey of all predators (except *G. nanum*), whereas *P. darwini* was preferred prey for owls only, and *O. degus* primarily for foxes and *B. virginianus*. Except for foxes, the remaining predators (i.e., owls) failed to demonstrate numerical responses to the changes in abundance of small

mammals. Only *B. virginianus* increased dietary breadth consistently in response to declines in mammal abundance (Jaksic et al. 1993). Foxes were the most omnivorous predators utilizing large quantities of fruits and seeds, particularly of *Schinus molle* when small mammal populations were low (i.e., 1990–1991; Castro et al. 1994). In addition, other predators known to prey on small mammals included a snake, *Philodryas chamissonis*, and a lizard, *Callopistes palluma*.

In summary, we documented the strongest numerical effects of predator exclusions on *P. darwini* and *O. degus* with only some interaction effects on *A. olivaceus*. Competitor (degu) exclusions resulted in the strongest effects on *A. olivaceus*. At the same time, diets of aerial and terrestrial vertebrate predators suggested the greatest collective predation on *A. benetti*, followed by *P. darwini* and *O. degus*.

DISCUSSION

Most evidence for strong predation effects on mammals has come from indirect approaches. Generally, these assume one of three forms. First, the effects of predators are studied in an artificial or seminatural enclosure (e.g., Dice 1947, Ambrose 1972, Marti and Hogue 1979, Brown et al. 1988, Kotler et al. 1988, 1991, Longland and Price 1991). Second, behavioral responses of prey species to conditions simulating altered predator risk are recorded (e.g., Thompson 1982a, b, Kotler 1984a, b, c, Brown 1989). Finally, comparisons are made between prey numbers, and predator numbers and diet over a period of time in order to infer the strength of the interaction (e.g., Pearson 1964, 1966, 1971, Fitzgerald 1977, Erlinge et al. 1983, Keith et al.

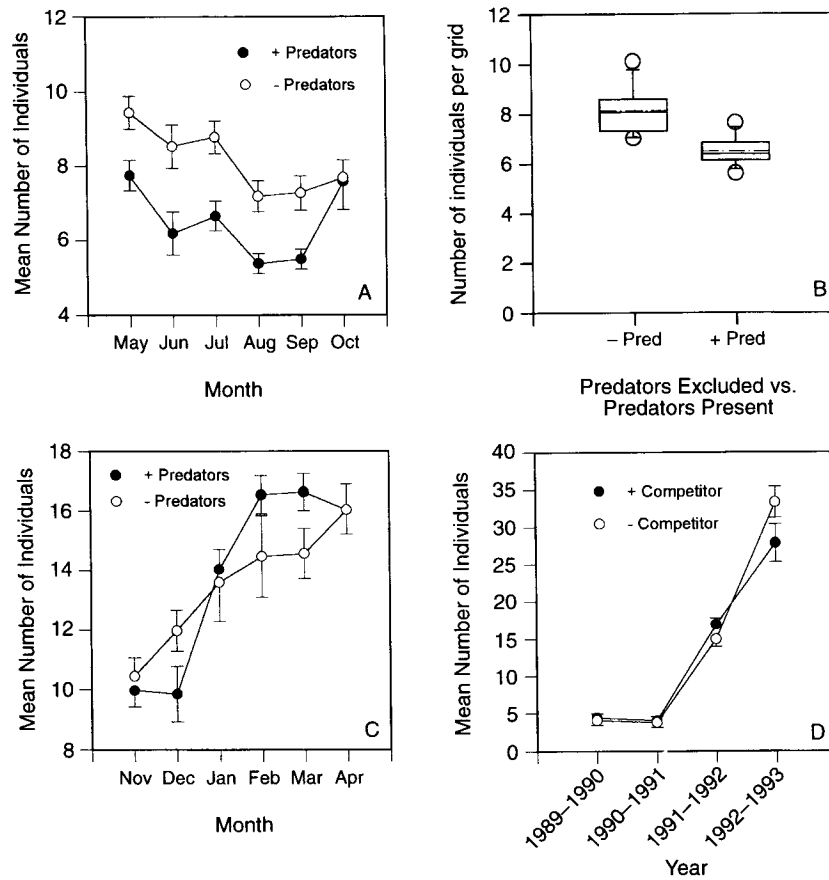


FIG. 5. Mean numbers of *Phyllotis darwini*/grid \pm 1 standard error by month (A) and Tukey box-plot for all months (B) of the wet season (May–October) of all years (1989–1993) on predator open (+predators) and predator exclusion (–predators) grids. Mean numbers/grid \pm 1 standard error by month (C) of the dry season (November–April) of all years (1989–1993) for predator open (+predators) and predator exclusion (–predators) grids, and by year (D) during the dry season on degu open (+competitor) and degu exclusion (–competitor) grids.

1984, Hanski et al. 1991, Jaksic et al. 1992). Experimental alteration of vertebrate predator densities in the field by their removal or exclusion from study areas in order to assess prey responses is much less frequent (e.g., Pearson 1964, 1966, 1971, Desy and Batzli 1989, Newsome et al. 1989, Desy et al. 1990, Pech et al.

1992) although more typical with aquatic invertebrates and lower vertebrates (re Kerfoot and Sih 1987).

Experimental field studies of competition among small mammal species are much more numerous (e.g., Dueser et al. 1989), but only a few studies have applied large-scale manipulations on a relatively long time scale as previously noted. Given that large fluctuations may occur in semiarid small mammal populations in response to extrinsic factors (e.g., Brown and Heske 1990, Meserve et al. 1995), it is important to fit the relative importance of competition within the context of intrinsic variations in small mammal densities over time.

The results confirm the importance of predation on numbers and survival of several species of small mammals including *Octodon degus* and *Phyllotis darwini*. Other species lacking numerical responses such as *Abrocoma bennetti* appeared to have greater survival or persistence in predator exclusion grids. Predation did not have a consistent effect on these species over time. Effects varied by season depending on the intrinsic pattern of increase, which in turn reflected an-

TABLE 3. Multiple comparisons of survivorship curves for species with an overall significant survival effect. Brackets connect treatments with significant or near significant differences based on a Bonferroni-adjusted $\alpha = 0.004$. Codes for treatments given in *Materials and methods*.

Species	Treatment			
	+D +P	+D –P	–D +P	–D –P
<i>P. darwini</i>				
<i>A. olivaceus</i>				
<i>O. longicaudatus</i>				
<i>A. bennetti</i>				

$P = 0.002$
 $P = 0.007$
 $P < 0.001$
 $P = 0.004$
 $P = 0.002$
 $P = 0.001$
 $P = 0.009$

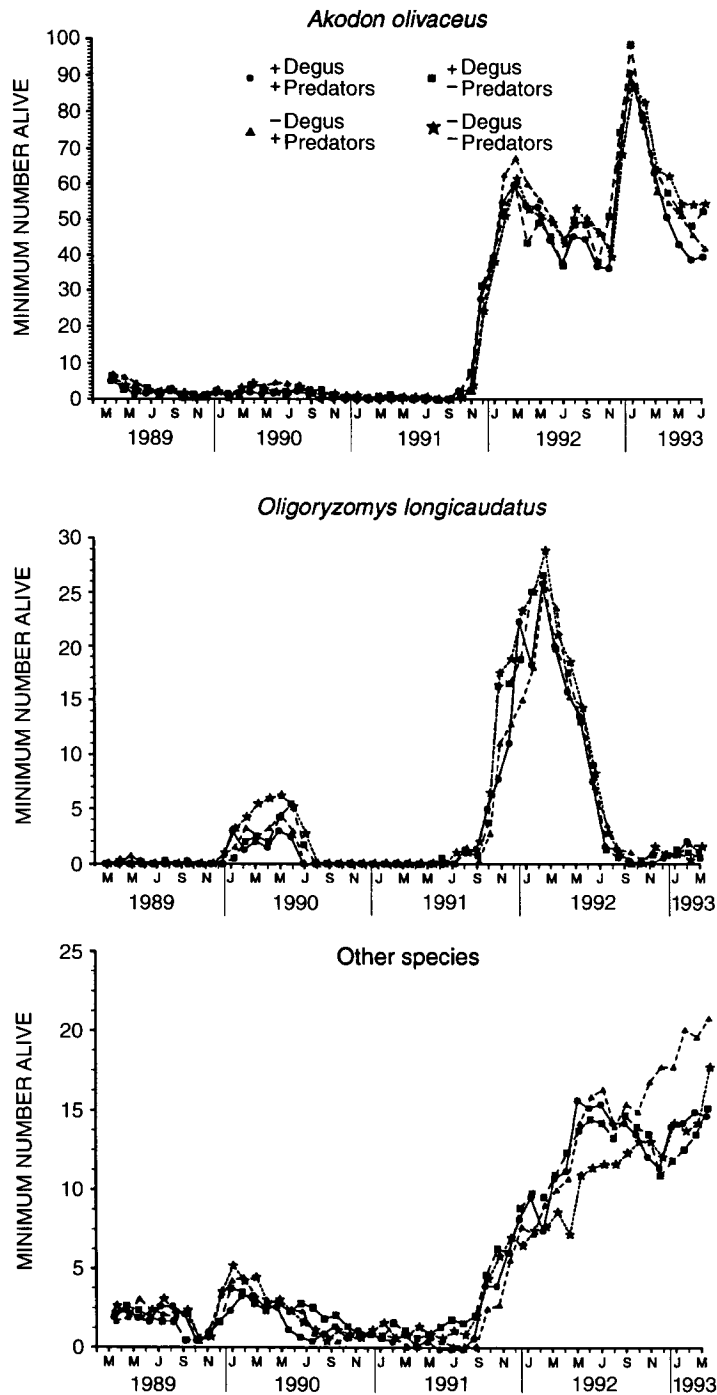


FIG. 6. Population trends of *Akodon olivaceus*, *Oligoryzomys longicaudatus*, and other species (*Abrothrix longipilis*, *Abrocoma bennetti*, and *Thylamys elegans*) during March 1989 through June 1993. Treatments indicated by symbols and adjacent labels. Standard errors omitted for clarity.

nual fluctuations and the effects of extrinsic events such as the 1991–1992 ENSO. Explanations for this varying role for predation may be that either there were no effects of predators at certain times, or that effects depend on intrinsic features of prey population dynamics. Initially, Meserve et al. (1993a) noted that predation effects on *O. degus* became more pervasive as populations declined generally through 1991. While this suggested that predation had greater numerical effects

when prey populations were low (e.g., Pearson 1966, 1971, Lidicker 1973, Akçakaya 1992), subsequent trends demonstrated even more dramatic effects during the *O. degus* increase in 1992–1993 (Fig. 2). Other investigators have argued that predators have dampening effects on prey population cycles (Goszcynski 1977, Southern and Lowe 1982, Erlinge et al. 1983), and noted strong correlations between predator abundance and the onset of cyclic declines and duration of

TABLE 4. Results of doubly within-subject repeated measures ANOVA of minimum number known alive per grid for *Akodon olivaceus* during the wet season and dry season. Within-subject *P* values are Huyhn-Feldt adjusted.

Source of variation	df	Wet season			Dry season		
		MS	F	P	MS	F	P
Between subject							
Predation	1	20.63	0.14	0.716	1.76	0.01	0.917
Competition	1	97.00	0.65	0.435	65.01	0.41	0.532
Predation × competition	1	72.63	0.49	0.498	57.04	0.36	0.558
Error	12	148.92			156.83		
Within subject							
Year	3	41 545.04	337.08	<0.001	102 304.85	914.58	<0.001
Year × predation	3	16.21	0.13	0.794	211.51	1.89	0.151
Year × competition	3	79.82	0.65	0.477	21.90	0.20	0.894
Year × predation × competition	3	27.45	0.22	0.714	14.74	0.13	0.937
Error (year)	36	123.25			111.86		
Month	5	58.22	11.58	<0.001	839.97	39.77	<0.001
Month × predation	5	20.47	4.07	0.003	9.75	0.46	0.803
Month × competition	5	23.38	4.65	0.001	44.59	2.11	0.076
Month × predation × competition	5	9.66	1.92	0.104	18.38	0.87	0.507
Error (month)	60	5.03			21.48		
Year × month	15	73.96	10.33	<0.001	1724.51	62.75	<0.001
Year × month × predation	15	9.95	1.39	0.223	22.77	0.83	0.551
Year × month × competition	15	13.21	1.85	0.093	32.35	1.18	0.328
Year × month × predation × competition	15	10.79	1.51	0.179	26.88	0.98	0.446
Error (year × month)	180	7.16			27.48		

population “lows” (Fitzgerald 1977, Henttonen 1985, Henttonen et al. 1987). It should be noted that all the latter studies involved small mammals with multiyear cycles.

Although varying over time, predation appeared to have more pervasive effects on species with more predictable patterns of seasonal reproduction and increase/decrease resulting in annual fluctuations (i.e., *O. degus* and *Phyllotis darwini*; Fig. 2). *A. bennetti* was also an important prey but was poorly represented in live trap censuses perhaps due to trap shyness. Species with less predictable annual fluctuations but greater magnitude and/or more rapid responses to the 1991–1992 ENSO (i.e., *A. olivaceus*, *Oligoryzomys longicaudatus*; Fig. 6) were less affected by predation. Other species that

showed no or weak numerical effects of predation demonstrated significantly greater survival in exclusion grids (i.e., *Abrocoma bennetti*; Fig. 4F). Thus, effects of predator exclusions may not be immediately manifest in differences in prey numbers, but rather by long-term changes in prey population structure including survival patterns that are more difficult to detect.

A general decline in predator density (particularly foxes) observed through mid-1992 did not result in large increases in its preferred prey (degus) then. Whereas numbers of non-degu species increased an order of magnitude or more beginning in late 1991, degus demonstrated a delayed increase probably due to intrinsic aspects of their reproduction (Meserve et al. 1995; Fig. 2). Similarly, whereas the relatively om-

TABLE 5. Results of singly within-subject repeated measures ANOVA of minimum number known alive per grid for *Oligoryzomys longicaudatus* during October 1991–November 1992 and for *Abrothrix longipilis* during November 1991–April 1993. Within-subject *P* values are Huyhn-Feldt adjusted.

Source of variation	<i>Oligoryzomys longicaudatus</i>				<i>Abrothrix longipilis</i>			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Between subject								
Predation	1	208.29	2.40	0.147	1	249.39	2.83	0.119
Competition	1	24.45	0.28	0.605	1	36.13	0.41	0.534
Predation × competition	1	23.14	0.27	0.615	1	98.00	1.11	0.313
Error	12	86.70			12	88.19		
Within subject								
Time	13	1247.56	77.17	<0.001	17	218.73	47.71	<0.001
Time × predation	13	32.61	2.02	0.128	17	6.78	1.48	0.157
Time × competition	13	5.06	0.31	0.818	17	8.25	1.80	0.069
Time × predation × competition	13	12.39	0.77	0.521	17	5.42	1.18	0.310
Error (year)	156	16.17			204	4.59		

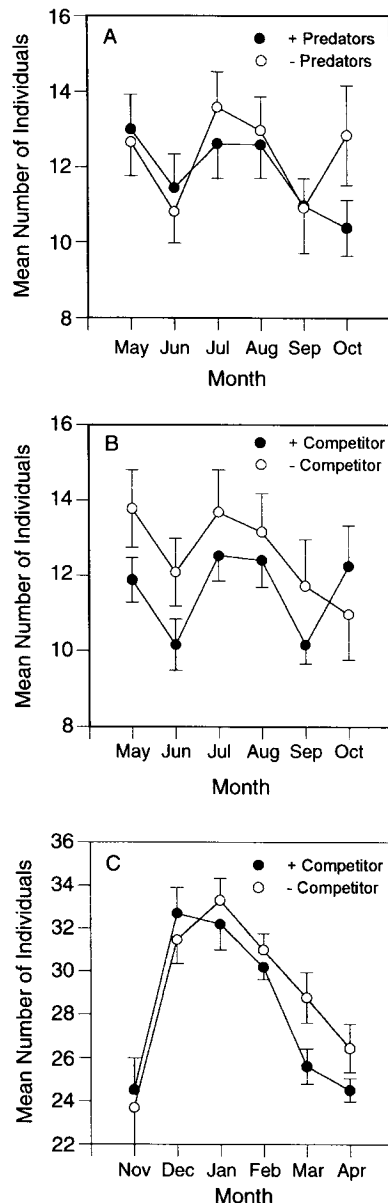


FIG. 7. Mean numbers of *Akodon olivaceus*/grid ± 1 standard error by month during the wet season (May–October) of all years (1989–1993) on (A) predator open (+predators) and predator exclusion (–predators) grids, and on (B) degu open (+competitor) and degu exclusion (–competitor) grids, and (C) during dry season months (November–April) of all years (1989–1993) on degu open (+competitor) and degu exclusion (–competitor) grids.

nivorous foxes had strong numerical responses to declining prey density through 1991, they exhibited a delayed increase to rapid prey density increases in late 1991 through 1992 (contra the prediction of Hanski et al. [1991] for generalized predators). The delay may have been due to the relative isolation of the park (and hence limited opportunities for immigration) as well as intrinsic delays in seasonal reproduction patterns of

foxes. These factors may confound the ability to detect significant overall effects of predation in short-duration experimental studies. Species showing weaker numerical responses to predator exclusions (i.e., *A. olivaceus*, *O. longicaudatus*) appeared to be less preferred prey among avian and mammalian predators (Jaksic et al. 1993). The lack of evidence of switching among these predators implicates the importance of strong prey preferences, which in turn may reflect differing prey population dynamics in the field, behavior, and energetic considerations. The diurnal, highly social degu as well as the larger, crepuscular/nocturnal *Abrocoma bennetti* may be more susceptible to fox predation, and the latter species was also overrepresented in nocturnal owl diets (Jaksic et al. 1993). They are also the largest small mammal prey available to foxes. In turn, the nocturnal *P. darwini* is significantly larger than *A. olivaceus* and *O. longicaudatus*, and appears to be the preferred prey for nocturnal owls.

Kotler (1984a, b, c), Kotler et al. (1992), Brown (1988, 1989), Brown et al. (1988, 1992), Lima and Dill (1990), Lima (1992), and Sih (1992) have emphasized the importance of prey behavioral responses to predators. We also have documented such responses of degus to predator exclusions. *O. degus* in predator open (control) grids utilize areas of high shrub cover significantly more, have a higher frequency of shorter, more angular runways, and have larger daily activity ranges than in predator exclusion grids (Lagos et al., *in press*). Similarly, *P. darwini* significantly alters nocturnal foraging patterns in response to flyover models and changes in illumination (Vásquez 1994). Other species probably also demonstrate similar effects of predation even when numerical or survivorship effects were not documented.

Our results indicate negative competitive interactions of *O. degus* particularly with *Akodon olivaceus*. This is intriguing given that *O. degus* is an herbivorous rodent, and has low temporal and dietary overlap with the continuously active, omnivorous *A. olivaceus* (Meserve 1981a, b). However, behavioral experiments performed in January–February 1992 similar to those of Brown (1988) and Brown et al. (1988) tested “giving up densities” (GUDs) or the level at which small mammals cease to remove a particular resource. *A. olivaceus* had significantly lower GUDs in degu exclusion vs. control grids indicating that they foraged more extensively in the former during daylight hours (J. A. Yunker and P. L. Meserve, *unpublished data*). Given the low dietary overlap and marked size differences present between these two species, the significant time \times competitor interactions detected in this study may indicate strong interference competition. We avoided the use of regression analyses of species abundances against each other (e.g., Crowell and Pimm 1976, Hallett and Pimm 1979, Hallett et al. 1983) recognizing that strong fluctuations in small mammal numbers due to extrinsic factors as well as intrinsic delays in individual species’

demographies may lead to spurious results (Brown and Heske 1990) in addition to other purely statistical concerns.

Finally, with the exception of *P. darwini* survivorship, we note the lack of significant predator \times competitor interactions in our analyses. Thus, the effects of predator and/or competitor exclusions appeared to be complementary or additive rather than multiplicative. Strong predation or competition effects did not appear to be coupled. Tentatively, this could be viewed as evidence for such biotic interactions having independent, decoupled effects on small mammal species in this assemblage.

We initially noted the importance of scale in ecology. Our study is currently the longest ongoing field manipulation in the temperate Neotropics, and has spanned a major climatic event (the 1991–1992 ENSO), which started 2 yr after its initiation. With adequate spatial and temporal scale, long-term studies enable interpretation of the effects of large-scale climatic events relative to those of local interactions at the individual or population level. Such studies enable the integration of information from small to large, and vice versa. As Levin (1992) noted, we may be interested in the consequences of life history adaptations such as dispersal and dormancy, which have implications for individual, population, and community level scales of observation. Finally, long-term studies provide opportunities for studying slow phenomena, rare events, and subtle and complex processes (sensu Franklin 1989, Pickett 1991). Similarly, hidden processes in the “invisible present” may only become evident with long-term studies (Magnuson et al. 1991). As our study indicates, manipulations may only reveal the importance of biotic interactions at relatively long temporal scales. The variable nature of pervasive interactions such as predation and competition may thus be “hidden” to the short-term observer, and lack of evidence for their influence on small mammal demography and other life history attributes misinterpreted as proof for the sole or overriding role of extrinsic events.

ACKNOWLEDGMENTS

We thank the following people who have served as technicians on the project: Kenneth L. Cramer, Sergio Herrera, Victor O. Lagos, Brian K. Lang, Bryan Milstead, Sergio S. Silva, Elier Tabilo, and Miguel-Angel Torrealba. Others have assisted in various aspects of fieldwork including Meredith Gooding, Alvaro Levicán, Valeria Salvatori, Gaia Vaglio, Victor Valverde, and Hernán Vásquez. Also, we appreciate the assistance of various Earthwatch volunteers in 1993. We are grateful to the Corporación Nacional Forestal, IV Region, and in particular to Waldo Canto and Juan 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 Graduate School, Northern Illinois University, the U.S. National Science Foundation (BSR-8806639, DEB-9020047, DEB-9318565), and the Fondo Nacional de Investigación Científica y Tecnológica (FONDECYT 90-0930 and 191-1150), Chile.

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