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Role of biotic interactions in a semiarid scrub community in north-central Chile: a long term ecological experiment

Rol de interacciones biológicas en una comunidad semiárida en Chile centro-norte: un experimento ecológico de largo plazo

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ABSTRACT

Previous studies of the Chilean mediterranean and semiarid regions have suggested a major role of predation, and plant-animal interactions in structuring small mammal assemblages, and in determining trophic interactions within the community. However, few long-term, large scale field experiments have been conducted in the temperate Neotropics, and such studies are needed to assess the generality of patterns largely derived from studies conducted in the Northern Hemisphere. Since 1988, we have been investigating the role of vertebrate predation, interspecific competition, and small mammal herbivory in a thorn scrub community located in a national park (Fray Jorge) in north-central Chile (Norte Chico). Large fenced enclosures are used to selectively exclude foxes and avian raptors, and the principal small mammal herbivore, *Octodon degus*. Initial results have shown significant effects of predator exclusions in numbers, survival rates, population structure, and behavior of degus. Although effects of excluding degus and/or predators have been mostly nonsignificant on other small mammal and plant species thus far, large increases have occurred in these groups as a result of an El Niño (ENSO) event in 1991-92. The importance of long-term, large scale studies of this nature is emphasized particularly in the Norte Chico where unpredictable rainfall events have dramatic effects on the community, and where the impact of desertification has been particularly severe.

Key words: Semiarid zone, small mammals, predators, experimental studies, desertification, El Niño (ENSO) events.

RESUMEN

Estudios previos de las regiones mediterráneas y semiáridas de Chile han sugerido que la depredación y las interacciones planta-animal tienen un rol importante en la estructuración de ensambles de pequeños mamíferos y en determinar las interacciones tróficas en la comunidad. Sin embargo, en los neotrópicos templados se han llevado a cabo pocos experimentos de terreno a gran escala y por largo plazo. Tales estudios son necesarios para juzgar la generalidad de patrones derivados mayoritariamente de estudios realizados en el hemisferio norte. Desde 1988 hemos estado investigando el rol de la depredación por vertebrados, competencia interespecífica y herbivoría de pequeños mamíferos en una comunidad arbustiva espinosa ubicada en un parque nacional (Fray Jorge) en Chile centro-norte (Norte Chico). Se usaron grandes exclusiones cubiertas y rodeadas con malla para excluir selectivamente a zorros y rapaces, y al principal pequeño mamífero herbívoro, *Octodon degus*. Los resultados iniciales han mostrado efectos significativos de la exclusión de depredadores en la densidad, tasas de sobrevivencia, estructura poblacional y conducta del degus. Aunque los efectos de excluir degus y/o depredadores han sido mayormente no-significativos en los otros pequeños mamíferos y plantas, han habido grandes aumentos en estos grupos como resultado del evento de El Niño (ENSO) en 1991-92. Se enfatiza la importancia de estudios de esta naturaleza a gran escala y por períodos prolongados, particularmente en el Norte Chico, donde eventos de lluvia impredecibles tienen dramáticos efectos en la comunidad y donde el impacto de la desertificación ha sido particularmente severo.

Palabras claves: Zona semiárida, pequeños mamíferos, depredadores, estudios experimentales, desertificación, los eventos de El Niño (ENSO).

INTRODUCTION

Much attention has been directed towards identifying the role of biotic interactions affecting community structure. The question often asked is to what extent is the presence, abundance or distribution of an organism in a particular community determined by processes

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such as competition, predation, parasitism, or other biotic interactions. Such interactions are frequently investigated separately or with emphasis on only a few species; yet, a species' population is more likely limited by several simultaneous interactions involving many species (Roughgarden & Diamond 1986, Lubchenco 1986). Further, processes such as competition, predation, and herbivory may be closely intertwined such that it is difficult to disentangle the effects of one interaction from those of another. Finally, taxonomic and geographical biases may influence the development of a general body of theory. Although it may appear that there has been a historical bias towards the study of higher vertebrates (i.e., birds and mammals) in the development of community ecology, in fact much more experimental work has been conducted on frequently more tractable and less mobile lower vertebrates, invertebrates, and plants. For example, Schoener (1983), and Connell (1983) cited only 29 (out of 164; 17.9%), and 11 (out of 72; 11.3%) experimental studies of interspecific competition, respectively, conducted with birds and mammals in their reviews. Similarly, experimental studies of predation are much more common among aquatic invertebrates, and lower vertebrates (see Kerfoot & Sih 1987 for a recent review). Sih *et al.* (1985) listed 139 studies of predation of which only 19 (13.7%) involved bird and/or mammals.

A geographical bias is also apparent. Neither Schoener (1983) nor Connell (1983) listed any experimental studies on interspecific competition from South America. Murúa *et al.* (1987) found only two previous manipulative studies on interspecific competition in mammals (i.e., August & Fleming 1984, Simonetti *et al.* 1985), and there is a paucity of experimental studies for the Southern Hemisphere generally. Although some recent studies have examined predation and herbivory in temperate Neotropical marine communities (e.g., Moreno & Sutherland 1982, Jara & Moreno 1984), none have experimentally examined the role of predation in higher vertebrates. The proceedings of the conference "International Workshop on Interactions between Trophic Levels: Towards a synthesis of North and South American Results" published in the Revista Chilena de Historia Natural (60[3], December 1987) has as a recurrent theme the absence of experimental studies conducted in South America, especially on biotic interactions among terrestrial vertebrates.

Observational and comparative approaches in the field are most often utilized in studies of factors influencing organism abundance and distribution (Krebs 1988). Long-term studies occasionally include "natural experiments" in which changing environmental conditions provide tests of the relative importance of biotic interactions such as competition and predation (e.g., Galápagos finches: Grant & Abbott 1980, Grant *et al.* 1985, Schluter & Grant 1984, Schluter *et al.* 1985; desert rodents: Larsen 1986). Especially with highly mobile small mammals, however, most experimental studies have focused on relatively short term, specific studies of their community ecology such as habitat selection (e.g., Rosenzweig 1973, Price 1978a, Harris 1984), seed partitioning (e.g., Lemen 1978, Price 1978b, 1985, Mares & Williams 1977, Reichman & Oberstein 1977, Reichman 1979, Price & Podolsky 1989), and interspecific competition (e.g., Joule & Jameson 1972, Cameron 1977, Lemen & Rosenzweig 1978, Montgomery 1981, Fox & Pople 1984, Dickman 1986, Fox & Gullick 1989). Only a few studies have applied large scale manipulations to small mammals on a relatively long time scale (e.g., Grant 1969, 1972, Krebs *et al.* 1969, Munger & Brown 1981, Brown & Munger 1985, Brown *et al.* 1986, Brown & Zeng 1989). The last four cited studies and those of Brown *et al.* (1979a, 1979b), and Davison *et al.* (1980, 1984, 1985) have emphasized interactions between granivorous rodents and other seed-eating groups such as ants and birds, as well as directed and indirect interactions with plants in the community.

Once the natural history of a particular group of mammals is sufficiently well known, a manipulative approach is crucial to understanding the role of biotic interactions and regulatory processes within the assemblage. Although field experiments may suffer from their smaller scale, and lack of control of independent variables (i.e. due to site, temporal, or weather variation) as compared to observational approaches, they offer a means of effectively isolating and testing specific questions regarding the structure of natural assemblages (Schoener 1983, Diamond 1986).

PROPERTIES OF CHILEAN MEDITERRANEAN AND SEMIARID SMALL MAMMAL ASSEMBLAGES

Intercontinental niche patterns

The mediterranean-type and semiarid regions of Chile and Argentina received considerable attention as a result of the major focus of the International Biological program (1967-1974) towards evidence for convergent properties between regions in the world. There is a replete literature on the results of these efforts (e.g., Di Castri & Mooney 1973, Mares 1975, 1976, Cody *et al.* 1977, Mooney 1977, Mooney *et al.* 1977, Orians & Solbrig 1977, Thrower & Bradbury 1977, Mares & Rosenzweig 1978, Ojeda 1989), but other workers have made significant contributions to our knowledge particularly of major vertebrate groups in Chile (e.g., Fulk 1975, Fuentes & Jaksic 1979a, 1979b, 1980, Jaksic *et al.* 1979, 1981a, 1981b, Jaksic & Fuentes 1980, Meserve 1981a, 1981b, Meserve *et al.* 1984, Meserve & Le Boulengé 1987). From these, intriguing patterns emerge with respect to the structure of small mammal assemblages in Chilean mediterranean/semiarid regions.

Cody *et al.* (1977) noted that although within-habitat diversities of small mammals are similar for mediterranean communities in California and Chile, between-habitat diversities are conspicuously lower in the latter area. Thus the same species tend to occur in many habitats in Chile, and there is very little reciprocal replacement by ecological similar forms in different habitats. In central Chile, these include the cricetid rodents *Akodon (Abrothrix) olivaceus* (olivaceous field mouse), *A. (Abrothrix) longipilis* (long-haired field mouse), and *Phyllotis darwini* (leaf-eared mouse), and the hystricognath octodontid rodent *Octodon degus* (degu). Members of several other species including *Oryzomys (Oligoryzomys) longicaudatus* (long-tailed rice rat), *Marmosa (Thylamys) elegans* (mouse opossum), and *Abrocoma bennetti* (chinchilla rat) tend to be more sporadic and/or highly localized in occurrence (Fulk 1975, Glanz 1977, 1982, 1984, Jaksic *et al.* 1981a; Meserve 1981a, 1981b, Meserve *et al.* 1983, 1984; Meserve & Le Boulengé 1987, Iriarte *et al.* 1989; all classifications follow Honacki *et al.* 1982).

Comparisons of niche utilization patterns among these species with those of California small mamals indicate that the former have conspicuously higher habitat overlap while dietary overlap is similar within faunas of the two areas (Glanz 1977, Meserve 1981a). Glanz (1977) and Glanz & Meserve (1982) showed that Chilean small mamals tend to demonstrate stronger patterns of habitat selection for areas of high shrub cover. These results suggest that Chilean small mammals do not fit the previously documented pattern of a greater importance of habitat vs. food partitioning, nor strong niche complementarity (cf. MacArthur 1972, Schoener 1974) for competition-structured communities. Microhabitat use is important, but Chilean small mammals tend to be similar in its use due to convergent effects of predation, food availability and the patchy nature of mediterranean-type communities (Glanz 1977, Meserve 1981a, Simonetti 1989a).

Another salient feature is that they show strongly defined feeding niches (Glanz 1977, Meserve 1981a, 1981b, Glanz & Meserve 1982, Meserve *et al.* 1983). Thus, in north-central Chile the four most common small mammals have different trophic positions; *Octodon degus* is an herbivore, *Phyllotis darwini* a granivore, *Akodon longipilis* an insectivore, and *A. olivaceus* an omnivore (Table 1: Meserve 1981b; these species constituted 94% of the captures at Parque Nacional Fray Jorge during 1972-1975: Meserve & Le Boulengé 1987). A second, less abundant species is present for each of the first three trophic specializations (Table 1). In general, Chilean small mammal assemblages along with those in the nearby Argentine Monte Desert demonstrate a lack of granivores, and a greater proportion of insectivorous plus herbivorous species (Glanz 1977, 1982, 1984, Mares & Rosenzweig 1977, 1978, Meserve 1981b, Morton 1985, Torres-Mura *et al.* 1989). There is little evidence for conspicuously different seed or insect availabilities in the Chilean mediterranean region (although Cody *et al.* 1977 and Mooney *et al.* 1977 suggested higher relative abundance of insects during

TABLE 1

Species, mean body weight and dietary specialization of small mammals in Fray Jorge National Park

Especies, peso promedio del cuerpo y especialización dietaria de pequeños mamíferos en el Parque Nacional Fray Jorge

Species	Mean weight (g)	Dietary specialization
Family Cricetidae		
Akodon olivaceus	32 ± 5	Omnivore
Akodon longipilis	54 ± 9	Insectivore
Phyllotis darwini	58 ± 14	Granivore
Oryzomys longicaudatus	24 ± 3	Granivore
Family Octodontidae		
Octodon degus	14 ± 21	Herbivore
Octodon lunatus	150 - 200	Herbivore
Family Abrocomidae		
Abrocoma bennetti	201 ± 46	Herbivore
Family Didephidae		
Marmosa elegans	23 ± 10	Insectivore

the dry season), nor significant differences in number of other granivorous groups such as birds and ants (Cody *et al.* 1977). The conspicuous absence of granivorous small mammals in South America as specialized as North American heteromyids may be simply an historical accident. Also, at least two myomorph rodents, *Phylloti darwini* and *Oryzomys longicaudatus*, are moderately granivorous in various Chilean communities (Table 1, Glanz 1977, Meserve 1981b, Murúa & González 1981, Meserve *et al.* 1988). Morton (1979) and Glanz (1982, 1984) discussed the prevalence of insectivory among temperate Southern Hemispheric small mammal assemblages. Aside from the mouse opposum (*Marmosa elegans*), the other major insectivorous group in Chile are akodont rodents.

Competition, predation, and herbivory

The foregoing does not support the view of a strongly competition-structured community at least among the numerically dominant species in mediterranean and semiarid Chile (but see Simonetti *et al.* 1985) or elsewhere such as in southern temperate rainforest (Murúa *et al.* 1987). An alternative explanation for patterns of habitat utilization among small mammals is that predation plays a major role in these regions. This view has been more forcefully advanced by Jaksic and co-workers (e.g., Jaksic *et al.* 1979, 1981b, 1992, Jaksic & Ostfeld 1983, Jaksic 1986, Jaksic & Simonetti 1987; see also Simonetti 1989a, 1989b). Mediterranean and semiarid Chile possesses a diverse predator assemblage of diurnal raptors, owls, mammalian carnivores, and snakes (Jaksic *et al.* 1981b), and small mammals are important prey items for most of these (Jaksic *et al.* 1981b, Jaksic 1986).

A number of important recent studies have shown significant effects by small mammal consumer groups on their plant resources in mediterranean/semiarid communities. Earlier literature documented important herbivore effects on plants in California (e.g., Biswell 1961, Davis 1967, Bartholomew 1970, Mills 1986). Similarly, Fuentes & Le Boulengé (1977), Jaksic & Fuentes (1980), and Fuentes *et al.* (1983, 1984) verified the existence of rapid effects of herbivorous small mammals including degus and introduced rabbits (*Oryctolagus cuniculus*) on both shrubby and herbaceus plants of the Chilean mediterranean scrub community. These effects may in turn be mediated by interactions between small mammal prey and their predators (Jaksic 1986). However, until recently, no study has attempted to distinguish these interactions using a methodology that separates the effects of predation from those involved in plant-small mammal interactions or competition.

AIMS OF THE PROJECT

This study which was initiated in 1988, focuses on three principal questions that are being examined with manipulative approaches in the field. Specifically these are:

(1) What is the role of predation in affecting small mammal demography, foraging activity, spatial distribution, and assemblage structure?

(2) What are the important effects of the principal small mammal herbivore, *Octodon degus*, on plant community composition and structure?

(3) What are the possible competitive effects (if any) of the largest and most herbivorous principal small mammal species (*Octodon degus*) on the remaining members of the small mammal assemblage?

We are addressing these questions in a community in which: (1) a morphologically and trophically diverse assemblage of small mammals is present; (2) a diverse taxonomic guild of avian and mammalian predators exists in high concentrations feeding primarily on small mammals; and (3) small mammals are known to feed on important vegetational components, and have been implicated to have strong community effects.

STUDY AREA AND METHODS

Study site

The study area is located within Parque Nacional Fray Jorge (71°40'W, 30°38'S) approximately 100 km S La Serena and 400 km N Santiago (IV Región), near the coast (Fig. 1). The park is a World Biosphere Reserve and contains approximately 10,000 ha of semiarid thorn scrub vegetation, and remnant fog forests (on coastal mountain ridges), which have been protected from grazing and disturbance since 1941. The flora of the lower elevational scrub zone is well-known (Muñoz & Pisano 1947, Hoffmann 1978, Muñoz 1985) and consists of spiny drought-deciduous and evergreen shrubs and an herbaceous understory on a predominantly sandy substrate. The plant association has been called the *Porlieria chilensis-Proustia pungens-Adesmia bedwellii* association for its most characteristics shrubs (Muñoz & Pisano 1947). 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 (mean January temperature = 24°C), but fog contributes significant additional moisture in many months.

The study area is "Quebrada de las Vacas" (240 m elevation) where a relatively homogeneous community of thorn scrub exists and where the work of Schamberger & Fulk (1974), Fulk (1976a, 1976b), Meserve (1981a, 1981b) and Meserve & Le Boulengé (1987) was concentrated. In addition to the small mammal assemblage here, there is a diverse group of predators present. The most prominent of these are the owls *Speotyto cunicularia, Tyto alba*, and *Bubo viriginianus*, several accipitrids and falcons, and the colpeo fox (*Pseudalopex culpaeus*). Predator concentrations within park boundaries are particularly high, probably because the park encloses the only significant expanse of undisturbed scrub community in north-central Chile. Most of the predators listed above have been noted as important predators of small mammals (Fulk 1976a; Jaksic *et al.* 1981b, Meserve *et al.* 1987, Jaksic *et al.* 1993).

Small mammal studies

Small mammal surveys were conducted starting in October 1988 in Quebrada de las Vacas using Sherman-type live traps set in lines parallel to the N-S axis of the valley. In early 1989, 16-75 m x 75 m grids (0.56 ha) were delineated each with 5 x 5 arrays of stations 15 m apart. Grid size was based on minimum trapping area necessary to detect members of the most common small mammal species (Table 1) especially during periods when densities are low (cf. Meserve & Le Boulengé 1987). Trapping was initiated on a monthly basis with two Sherman-type traps/station set for four nights/month at 30 day intervals using standard mark and recapture techniques. Census duration has been 4-6 nights/month/grid. Traps are checked twice daily in early morning and late afternoon hours (fall through spring), or thrice daily (summer). Shelters are placed over traps to minimize exposure to sun as well as rainfall. Animals are marked with ear tags or leg bands, and standard data are taken on species, number, trap location, sex, reproductive condition, weight, and special remarks. Data from small mammal censuses have been analyzed on the NIU mainframe computer using the CMR (capture-mark-recapture) programs of Le Boulengé (1985). This package produces data summaries such as the Calender of Captures (Petrusewicz & Andrzejewski 1962), sex ratios, reproductive condition, Minimum Number Known Alive (Krebs 1966) tabulations, plots of traps visited, and weights at first capture. Higher level analyses are available for trappability analysis, density and home range estimations, disappearance rates, and weight dynamics; an example of its application is provided in Meserve & Le Boulengé (1987).

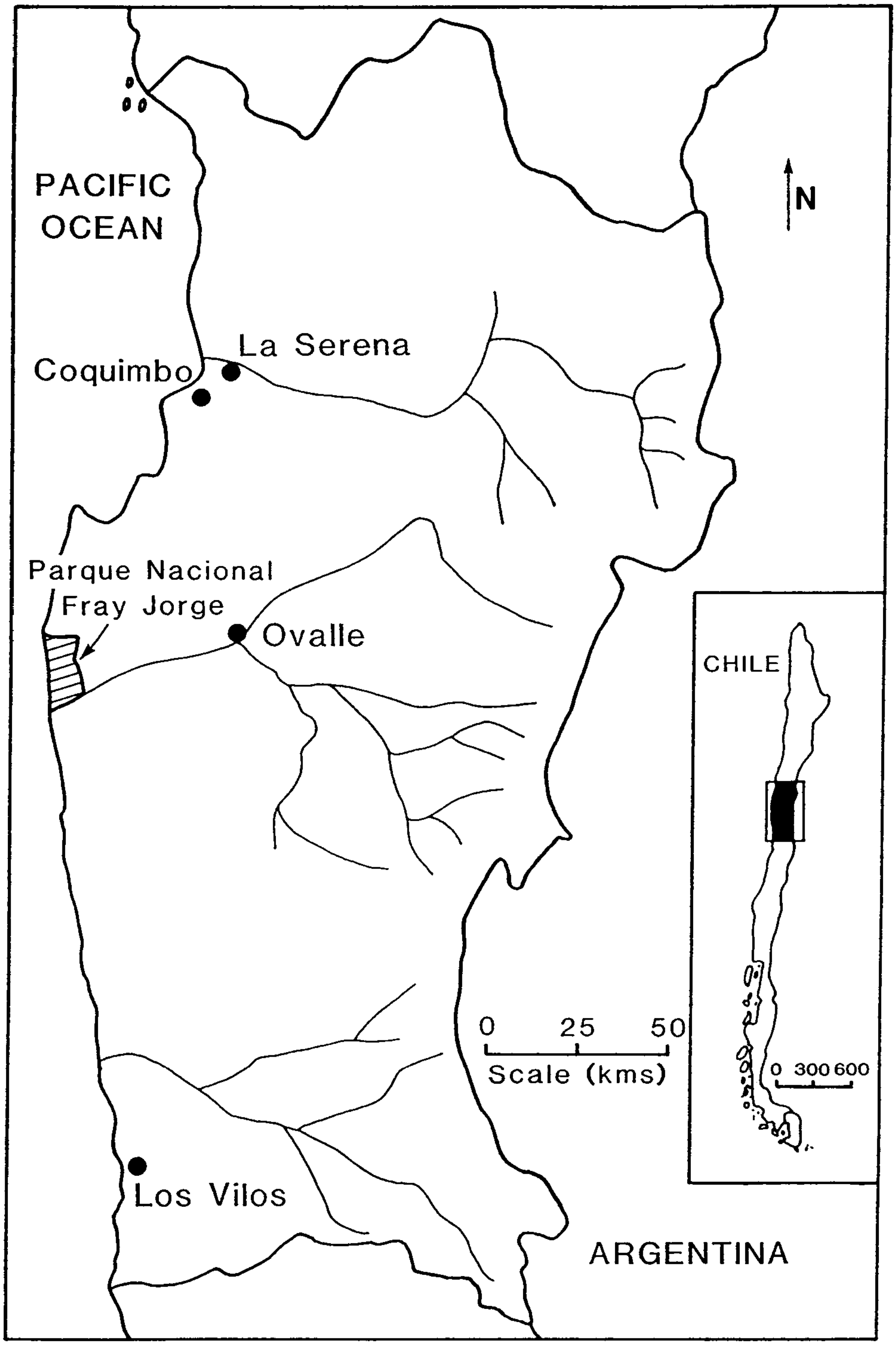

Fig. 1: Map of the IV Region (Coquimbo) in north-central Chile showing location of Parque Nacional Fray Jorge.
Mapa de la IV Región (Coquimbo) en Chile centro-norte mostrando la ubicación del Parque Nacional Fray Jorge.

Predator studies

In addition to monthly small mammal censusing, data have been collected continuously on predator diets. Since November 1988 fox scats (*Pseudalopex culpaeus*) and owl pellets have been collected monthly from the study area (grids plus intervening road and vicinity), and active burrows (i.e., *Athene cunicularia*) and roosts nearby. Carnivore feces and raptor pellets are examined in the laboratory and prey remains identified to species level using a reference key and voucher specimens. Tabulations have also been made on numbers of predators sighted during trap checks and detected during monthly monitoring of olfactory lines transecting the study area using commercially available scents (more details provided in Jaksic *et al.* 1993). Additionally, owl playback calls have been conducted at fixed sites in the study area to monitor strigiform activity. Finally, studies of the effects of predators on small mammal microhabitat use are being conducted. These have focused on the activity of *Octodon degus* in predator-open and predator exclusion plots using smoked tiles placed under and between shrubs (Justice 1961), and flourescent powder tracking (Lemen & Freeman 1985).

Plant studies

Three procedures for monitoring plant community changes have been employed. To determine shrub and perennial herbaceous cover, four permanent parallel lines (75 m long each) located 15 m apart are used on each grid with 150 points at 50 cm intervals. These lines were monitored every four months in 1989 and every three months from 1990 on, using the point intercept technique (Mueller-Dombois & Ellenberg 1974). To measure the cover of annuals and geophytes, the point intercept technique is used along 10 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. This sampling effort is consistent with the short life spans and species turnover patterns observed among herbaceous annuals in other semi-arid regions (Gutiérrez & Whitford 1987a, 1987b; Gutiérrez *et al.* 1988). Soil samples have been collected every four months since April 1989 using 20 randomly located collecting tubes (3 cm diameter x 5 cm depth = 35.35 cm^3) in each of the 16 grids. Previous sampling to 6 cm has demonstrated that less than 10% of the seeds are found in the 4-6 cm interval (Meserve 1981a). Samples have been returned to the laboratory, separated initially by mechanical sieving, and identified to species whenever possible using seeds collected from plants in the field as a reference.

Experimental setup

The basic experimental design is as follows:

1) Four plots have low (1.0 m high) fencing buried approximately 40 cm into the ground with enlargements of the 2.5 cm mesh cut in the chicken wire (yielding an approximately 5 cm d hole) at ground level to allow access by all small mammals and predator (control plots, +D +P);

2) four plots have high (1.8 m h) fencing buried 40 cm with holes in the fencing and polyethylene netting (ca. 15 cm mesh size) suspended 2-3 m overhead, to exclude predators, but at the same time allow small mammal access (including degus) (predator exclosure plots, +D –P);

3) four plots have low (1.0 m h) fencing buried 40 cm without holes so as to exclude the principal small mammal herbivore, the degu (*Octodon degus*), but not other small mammals or predators (degu exclosure plots, –D +P); and,

4) four plots have high (1.8 m h) fencing buried 40 cm with overhead netting, but without holes in the fencing to exclude both degus and predators (degu and predator exclosure plots, –D –P).

Fig. 2 shows the orientation and identity of the experimental units described above. For purposes of statistical analysis, the design may be considered a 2 x 2 factorial design with the factors being predation (presence or absence) and herbivory (presence or absence).

Due to variation between plots with respect to initial densities of degus in March-May 1989, a partially stratified procedure was used to assign treatments and replicates (Steel & Torrie 1980). ANOVAs for repeated measurements (SAS Institute, Inc., Cary, NC) are used for plant cover data after applying angular transformation to percentages. Small mammal data are analyzed on the Northern Illinois University mainframe computer using one– and two-way MANOVAs (GLM procedure SAS) in order to differentiate time dependent effects resulting from interdependency of sequential census data from main

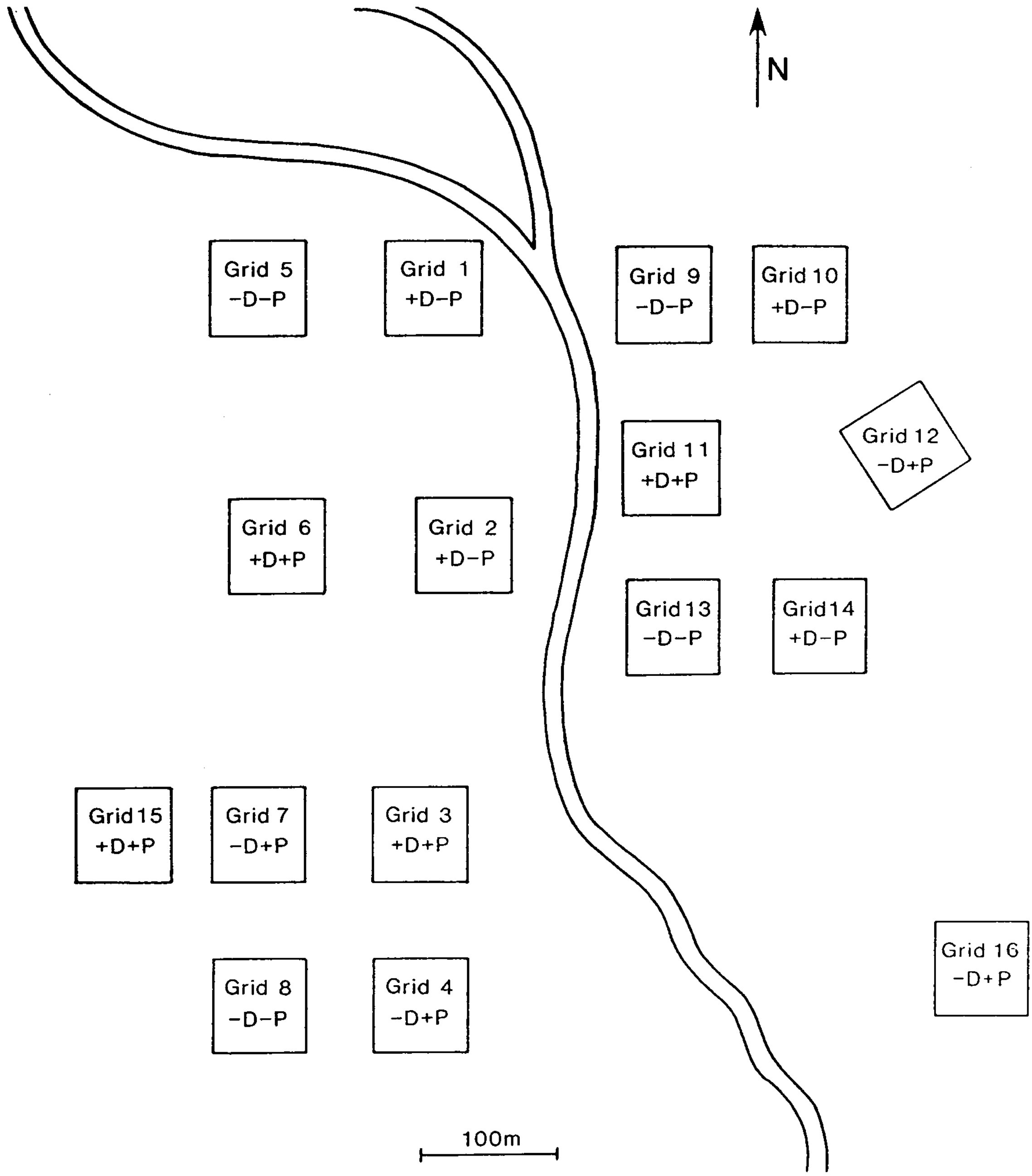

Fig. 2: Orientation and identity of experimental units in Quebrada de las Vacas, Parque Nacional Fray Jorge. Letters within grid outlines denote experimental treatment: +D, -D and +P, -P refer to presence or absence of degus (herbivores) and predators, respectively.

Orientación e identidad de las unidades experimentales en la Quebrada de las Vacas, Parque Nacional Fray Jorge. Las letras dentro de las unidades denotan los tratamientos experimentales: +D, -D y +P, -P se refieren a la presencia y ausencia de degus (herbívoros) y depredadores, respectivamente.

treatment effects. Due to the small number of replicates relative to number of time periods available, data have been analyzed separately for consecutive three-month blocks corresponding approximately to the major seasons in Fray Jorge; fall (March-May), winter (June-August), spring (September-November), and summer (December-February). Since construction of the fences was not completed until late May 1989, and degu removals were not initiated until then, the first three months (March-May 1989) constitute a pre-test period. Predator scat and pellet data are analyzed for the same periods, noted above using X^2 goodness of fit tests comparing observed frequencies of prey in predator diets and trap-revealed numbers on control (+D +P) grids. Cell frequencies for prey categories are pooled when less than 5.

PRELIMINARY RESULTS

We are currently in our fourth year of work; some findings have been reported or are in review (e.g., Contreras & Gutiérrez 1991, Contreras *et al.* 1993, Gutiérrez *et al.* 1993a, 1993b, Jaksic *et al.* 1993, Meserve *et al.* 1993). The purpose of this report is not to present a detailed description of major results but rather to provide a theoretical and empirical framework for the project as well as detail its organization and structure. However, three examples of results serve to illustrate the complexity of the ongoing work and the importance of long-term projects in the northern semiarid region due to effects of extrinsic events.

Predation effects

Meserve *et al.* (1993) documented major effects of predator exclusions on the population sizes, survival, and age structure of *Octodon degus*. Specifically, although numbers of *O. degus* were nonsignificantly different ($P > 0.05$) in predator exclusion vs. control grids (– Predators [+D –P], and + Predators [+D +P], respectively, Fig. 3) through mid-1991, there was a trend for greater numbers of degus

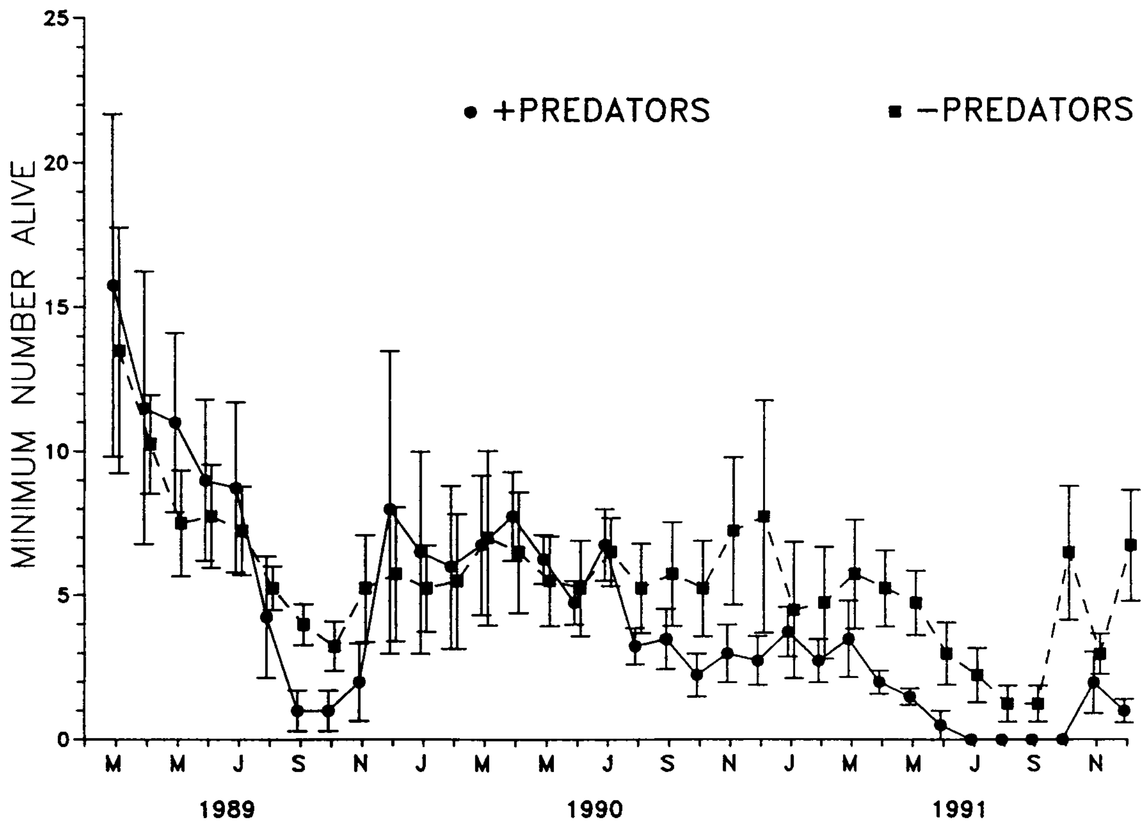

Fig. 3: Mean minimum number known alive trends for *Octodon degus* in Fray Jorge on control grids (solid dots, +Predators or +D +P), and predator exclusion grids (solid squares, –Predators or +D –P) during March 1989-December 1991. Exclusions of predators started in March 1989. Vertical lines and intervals include one standard error of the mean for four grids/treatment.

Tendencias promedio del número mínimo conocido vivo para *Octodon degus* en Fray Jorge en las grillas control (círculos llenos, +Depredadores o +D +P), y en las grillas de exclusión de depredadores (cuadrados llenos, –Depredadores o +D –P) durante marzo 1989-diciembre 1991. La exclusión de depredadores comenzó en marzo de 1989. Las líneas verticales e intervalos incluyen un error estándar del promedio para cuatro grillas/tratamiento.

in predator exclusion grids during September-November 1989 and 1990. Since these trends did not persist, *in situ* reproduction and immigration was sufficient to compensate for predator losses in predator open grids. However, beginning in September-November 1991, differences became significant (MANOVA $F_{1,6} = 8.11, P = 0.029$) and have become more persistent. Thus, during a period when prey numbers became low (Fig. 3), strong predator exclusion effects have become evident. In addition, degu survival differences were present even when numerical differences were not (Fig. 4). Survival of adult degus is significantly longer in predator exclusion grids (Cox-Mantel test for comparison of exponential survival distributions, $Z = 2.59, P = 0.01$). During the same period, foxes (*Pseudalopex culpaeus* showed a significantly higher proportion of degus in their feces relative to proportions in live-trapped populations (Jaksic *et al.* 1993). At the same time, V. Lagos (unpubl.) has documented greater use of microhabitats under shrubs by *O. degus* using smoked tile tracking; in addition, degus from predator exclusion grids also show greater use of open microhabitats. This trend has been confirmed by results from fluorescent powder tracking. Thus, predators have important effects on numbers, survival, population structure, and behavior of degus in the field; numerical effects in particular may be transitory and dependent on absolute prey abundances in the field. This study is one of the few that has directly documented prey responses to predator exclusions in the field (see also Pearson 1964, 1966, 1971, 1985, Desy & Batzli 1989, Newsome *et al.* 1989). However, the numerical responses of several other small mammal species to predator exclusions have been nonsignificant and/or seasonal, suggesting a lesser importance of predation in their population biology.

Climate effects on small mammals and plants

Superimposed on the above changes, however, have been important climatic events. After a normal rainfall year in 1989 (89 mm), and a below normal year in 1990 (32 mm), 1991

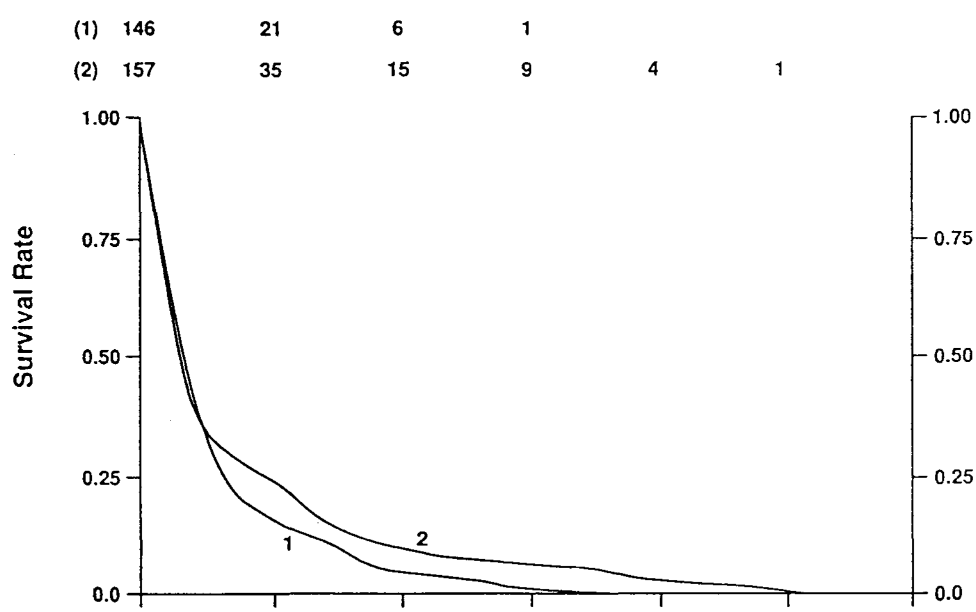

Fig. 4: Survival rates of degus on control or predator open (+D +P; "1") and predator exclusion (+D –P; "2") grids between June 1989 and November 1991; numbers across top of graph indicate numbers of individuals surviving cumulative five month periods.

Tasas de sobrevivencia de degus en las grillas control o abiertas a los depredadores (+D +P; "1") y en grillas con exclusión de depredadores (+D –P; "2") entre junio de 1989 y noviembre de 1991; los números atravesados arriba del gráfico indican número de individuos sobrevivientes acumulados en períodos de cinco meses.

was extremely wet (233 mm), and a similar trend has occurred in 1992. This appears to be a consequence of an El Niño Southern Oscillation (ENSO) event which has affected most of mediterranean and semiarid zone of central and northern Chile. Large increases in the numbers of most small ammmal and herbaceous plant species have been observed. For example, numbers of *Akodon olivaceus* have increased more than an order of magnitude since late 1991 (Fig. 5); this trend is continuing to date; other small mammal species such as *Oryzomys longicaudatus* and *Phyllotis darwini* have shown smaller and more protracted responses in population numbers. Interestingly, responses of *Octodon degus* through 1991 were small (Fig. 3) indicating possible biological differences in the ability of caviomorph and/or larger sized rodents to respond rapidly to extrinsic events.

Whereas total shrub cover has been relatively constant over three years of observation and similar to the figures reported by Meserve (1981a) collected in 1974 (59-60% cover), some perennial shrub species such as *Proustia pungens*, *Chenopodium petiolare* (a suffruticose perennial found in the understory and shrub margins), and *Anisomeria littoralis* have shown significant increases in cover in 1991 probably as a direct consequence of high rainfall. A total of 52 herbaceous species were recorded during monthly plant sampling between June-December 1991. Total annual cover peaked at 70-90% in October 1991, almost four times the plant cover in 1989. Nineteen species were recorded for the first time; many

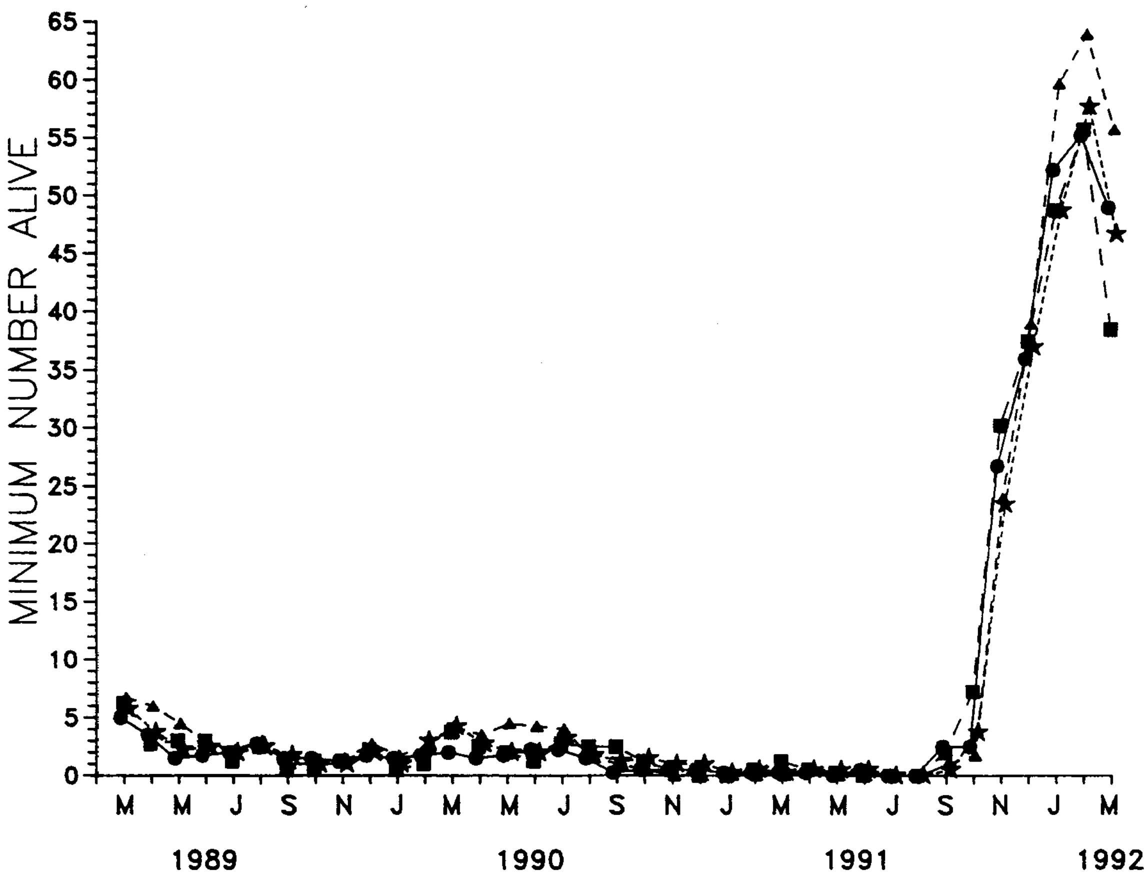

Fig. 5: Minimum number known alive trends for *Akodon olivaceus* in Fray Jorge during March 1989-March 1992. Symbols denote mean numbers of individuals for 4 replicate grids/treatment; solid dots = +D +P, solid triangles = –D +P, solid squares = +D +P, and solid stars = –D –P. Standard error bars have been omitted for clarity.

Tendencias del número mínimo conocido vivo para *Akodon olivaceus* en Fray Jorge durante marzo de 1989-marzo de 1992. Los símbolos denotan números promedios de individuos para 4 grillas-réplicas/tratamiento; círculos llenos = +D +P, triángulos llenos = –D + P, cuadrados llenos = +D –P y estrellas llenas = –D –P. Los errores estándar se han omitido para más claridad.

of these new species were restricted to areas under bushes probably reflecting high water and/or leached nutrient requirements. The most abundant herbaceous species was *Plantago hispidula*, which reached a maximum cover of between 23 and 33% on some plots. The most notable increment was observed in *Moscharia pinnatifida*, which reached a peak of between 28-40% cover in August 1991 (vs. < 2% in 1989 an 1990) sharing dominance with *P. hispidula*. Whereas *P. hispidula* was present in open areas, *M. pinnatifida* was restricted to areas under *Porlieria chilensis* and completely absent from open areas. The third most abundant herb was *Schizanthus litoralis* (10-15% cover in August 1991, a species not found during 1989-1990) followed by *Oxalis* spp. with 4-7% cover in August, almost ten times the cover reached by these species in 1989. Although treatment responses of herbaceous plants have been generally nonsignificant (i.e., $P > 0.05$), this is not surprising given the protracted nature of plant community responses in other herbivore exclusion experiments (e.g., Inouye *et al.* 1980, Davidson *et al.* 1984, Brown 1986).

Seed bank responses

Seeds of 55 species of plants have been identified in different treatment plots (approximately 80% of the seeds collected). Seeds of *Chenopodium petiolare*, *P. hispidula* and *M. pinnatifida* have been the most abundant. Grouping the seeds by category, only perennial herbaceous seeds have shown significant differences in predator and degu exclusion treatments. Depending on period, seeds of individual herbaceous species such as *Erodium* spp., *Moscharia pinnatifida*, and *Silene gallica* were more abundant in the degu-present (+D) plots in 1991; on the other hand, *Schizanthus litoralis* seeds were more abundant in –D +P plots than in other treatments. These results indicate that changes in seed abundances are complex and often demonstrate a delayed response as compared to abundance of seedlings and mature plants. More generally and similar to small mammals, extrinsic events such as extraordinarily high rainfall can superimpose an additional set of factors that may mask experimental treatment effects.

RELEVANCE OF THE PROJECT

The importance of long-term, large-scale studies

This description of some of initial results of our project, now in its fourth year, demonstrates the importance of large scale, long-term community studies particularly in the Chilean mediterranean and semiarid region. Traditionally, the short duration of most studies in this region has hindered their ability to resolve the relative importance of intrinsic (i.e., biotic interactions) vs. extrinsic factors. For example, had this study terminated in mid-1991 (after 2+ years; a common duration for small mammal and plant community studies), we would have not detected their large responses as a consequence of the 1991-1992 El Niño (ENSO) event. Further, effects of specific experimental treatments such as that of predator exclusions on numbers of their principal prey, the degu, did not become significant nor persistent until late 1991 (although survival differences were evident earlier). As to the importance of scale, it may be noted that use of smaller plots such as is typical in many community studies would have failed to detect representatives of many small mammal species during drought periods when their densities fall very low (i.e., 1990). As a case in point, in mid-1991 densities of *A. olivaceus* fell to ca. 1 individual/plot (Fig. 5); use of smaller plots would have made it unlikely that we could have detected *any* individuals during such periods. Therefore,the conclusion seems unavoidable that long-term studies with sufficiently large spatial scales of measurement can provide a comprehensive understanding of the relative importance of intrinsic vs. extrinsic factors as major forces influencing community structure.

Implications of the project for desertification

The importance of this study may also be emphasized with respect to the continuing desertification process in the Chilean Norte Chico region where the study site is located (Bahre 1979, Fuentes & Hajek 1979, Schofield & Bucher 1986). Historically, mean annual rainfall in Fray Jorge has declined from nearly 250 mm in the 1960's, to 129 mm by 1973-75, and the current 85 mm (Meserve & Le Boulengé 1987). Similar to previous decades, there have continued to be sporadic high rainfall years associated with El Niño events (e.g., 1972, 1983-84, 1986-87, and 1991-92). In spite of this, total perennial shrub cover has remained constant in the park since at least 1973. Outside the park, on the other hand,a continuing process of habitat degradation has been exacerbated by overgrazing by goats, perennial shrub removal, and marginal cultivation. Thus, the park represents an island of biodiversity retaining much of the character of the original surrounding landscape.

Strategies for reversing the desertification process have focused on revegetation of denuded areas with monocultures of introduced or formerly nondominant shrub species to stabilize soils. However, such solutions have failed to take into account the integral nature of the original community, its inherent faunal and floral diversity, and its resilience in response to long term climatic events. Farmers and ranchers around the park continue to actively employ herbicides, pesticides, and vertebrate predator control measures. The latter efforts especially have strong effects on park wildlife such as native carnivores, which foray out during times of low food availability in the park. Clearly, in addition to providing a comprehensive view of the nature and dynamics of the original community in this area, this study can contribute to the development of a comprehensive restoration policy especially in areas badly affected by past misuse. In addition to mitigating human impact, it will be necessary to promote a policy of native predator protection and exclusion of domestic livestock in denuded areas in order to reestablish stable, persistent communities in severely impacted regions. As our study is beginning to show, small mammal herbivores, their predators, and indigenous vegetation are closely intertwined and cannot be viewed as isolated components of the ecosystem. As we follow trends in the aftermath of a high precipitation event (1991-92), we expected to be able to observe magnified effects of our experimental treatments using the results of the first three years as a baseline for comparisons.

FUTURE DIRECTIONS

Our project offers unique opportunities to conduct research within the context of a long-term, large scale ecological experiment in an undisturbed, natural setting. In addition to the efforts described here, new directions for research include the study of physiological responses of organisms to predation, the importance of other trophic and taxonomic groups such as granivorous ants and birds, and the "top-down" response of vertebrate predators such as foxes to changing prey availability. We welcome interactions with interested ecologists everywhere (both students and researchers) and encourage them to take advantage of the many opportunities for future research. Of course, all proposals require specific prior approval by the Corporación Nacional Forestal, and must be compatible with the ongoing research program and the overall goal of minimizing impact on the unique fauna and flora of Parque Nacional Fray Jorge.

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