

## Original papers

# Effects of vertebrate predation on a caviomorph rodent, the degu (*Octodon degus*), in a semiarid thorn scrub community in Chile

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**Abstract.** The effects of vertebrate predation have been monitored since 1989 on 16 replicated 0.56 ha study plots in a semiarid thorn scrub community in north-central Chile. Using fences of different heights with and without holes and suspended game netting to alter principal predator (foxes and raptors) and large rodent herbivore (*Octodon degus*) access, four grids each have been assigned to the following treatments: 1) low fencing and holes allowing free access of predators and small mammals; 2) low fencing without holes to exclude degus only; 3) high fencing and netting with holes to exclude predators only; and 4) high fencing and netting without holes to exclude predators and degus. Small mammal population censuses are conducted monthly using mark-recapture techniques. Degu population trends during 1989 and 1990 showed strongly but nonsignificantly lower numbers in control plots during months when densities were characteristically low (September–November) for this seasonally reproductive species; since March 1991, differences have become persistent and increasingly significant. Predators appear to have greater numerical effects when their prey populations are low. Survival times of degus, particularly established adults, were significantly longer in predator exclusion grids during the 2½ years of observation; thus, predation also affects prey population structure.

**Key words:** Vertebrate predation – Small mammals – Semiarid zone – Neotropical mammals – Chile

Predation has been suggested to be a major biotic interaction influencing the population biology and assemblage structure of birds and mammals; yet they have been infrequent subjects of experimental studies. Sih et al. (1985) found only 19/139 (13.7%) experimental studies of predation involved bird or mammals. Most evidence for strong predation effects has therefore come

from indirect approaches. Generally these assume three forms; first, the effects of predators are studied in artificial or seminatural enclosures (e.g., Dice 1947; Ambrose 1972; Marti and Hogue 1979; Kotler et al. 1988, 1991; Brown et al. 1988; Longland and Price 1991). Alternatively, 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. 1984; Sinclair et al. 1990; Hanski et al. 1991; Jaksic et al. 1992).

A more direct approach, however, involves experimentally altering vertebrate predator densities in the field by removal or exclusion from study areas in order to assess prey responses. Although frequently done with aquatic invertebrates and lower vertebrates (Kerfoot and Sih 1987), there are few examples among birds and mammals (i.e., Pearson op.cit.; Marström et al. 1988, 1989; Desy and Batzli 1989; Desy et al. 1990; Newsome et al. 1989; Pech et al. 1992).

Additionally, most experimental field studies with birds and mammals are short-term; yet, responses of vertebrate populations to manipulations may be long-term. For example, smaller Chihuahuan Desert granivorous rodents and plants showed protracted responses to exclusion of larger granivores, and consumers, respectively (Munger and Brown 1981; Brown and Munger 1985; Brown et al. 1986).

Previous work in Chile suggested that competition among numerically dominant small mammal species is relatively unimportant in the mediterranean scrub and semiarid zones (Glanz 1977; Glanz and Meserve 1982; Meserve et al. 1981a, b; Meserve and Le Boulengé 1987; Iriarte et al. 1989), and in southern temperate rainforests (Murúa et al. 1987). Conversely, predation seems more important especially in explaining convergent patterns of habitat utilization among small mammals (e.g., Jaksic et al. 1979, 1981; Jaksic and Ostfeld 1983; Jaksic 1986;

Simonetti 1989a, b). Mediterranean and semiarid Chile possesses a diverse predator assemblage of raptors, mammalian carnivores, and snakes (Jaksic et al. 1981), and small mammals are important prey items for most of these (Jaksic et al. 1992, 1993). Despite these suggestive results, Murúa et al. (1987) found only two previous experimental manipulations of small mammals in the temperate Neotropics, both involving interspecific competition. Jaksic (1987), and Jaksic and Simonetti (1987) noted the lack of experiments on the role of predators in South America generally. Thus, while major theories have been proposed on the relative importance of biotic interactions, physical factors, and life history traits in explaining community structure (e.g., Hairston et al. 1960; Menge and Sutherland 1976; Sih et al. 1985; Schoener 1986a, b, 1989), the most species-rich biogeographic region is largely unstudied.

In 1989, a large scale experimental study was initiated in a semiarid scrub community in north-central Chile to assess the importance of major biotic interactions including predation and herbivory in the community. Herein we describe results that show important predator exclusion effects on a medium-sized (140–160 g) caviomorph rodent, the degu (*Octodon degus*) which often makes up the majority of small mammal biomass in central and north-central Chilean assemblages (Meserve and Le Boulengé 1987; Iriarte et al. 1989; Jiménez et al. 1992).

## Methods

The study area is located in a valley ("Quebrada de las Vacas"; 240 m) near the coast in Fray Jorge National Park, Chile (71° 40' W, 30° 38' S; Limarí Province, IV Region) approximately 100 km S La Serena and 350 km N Santiago (also described in Fulk 1975; Meserve 1981a, b; Meserve and Le Boulengé 1987; Meserve et al. 1993). This park contains ca. 10000 ha of semiarid thorn scrub vegetation and isolated fog forests (on coastal mountain ridges), which have been protected from grazing and disturbance since 1941. The flora of the lower elevational thorn scrub zone consists of relatively homogeneous spiny drought-deciduous and evergreen shrubs and an herbaceous understory on a predominantly sandy substrate (Muñoz and Pisano 1947; Muñoz 1985; Hoffmann 1989). 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.

Small mammals present in the study area in addition to *Octodon degus* include four sigmodontine rodents (*Akodon olivaceus*, *A. longipilis*, *Phyllotis darwini*, and *Oligoryzomys longicaudatus*), three caviomorph rodents (*Abrocoma benetti*, *Spalacopus cyanus*, and *Octodon lunatus*), and a marsupial (*Marmosa elegans*). A diverse predator assemblage includes the owls *Athene cunicularia*, *Bubo virginianus* (Strigiformes: Strigidae), and *Tyto alba* (Strigiformes: Tytonidae), and the culpeo fox (*Pseudalopex culpaeus*; Carnivora: Canidae). All are important predators of small mammals in the study area (Fulk 1976a; Meserve et al. 1987; Jaksic et al. 1992, 1993), and are particularly abundant within park boundaries probably because it has the only significant expanse of undisturbed semiarid scrub in coastal north-central Chile.

The experimental design is as follows:

1) four control plots (C) have low (1.0 m high) chicken wire fencing buried ca. 40 cm into the ground with enlargements of

the 2.5 cm mesh in the wire yielding a ca. 5 cm d hole every 1–2 m at ground level allowing all small mammal and predator access;

2) four predator exclusion plots (-P) have high (1.8 m h) fencing buried 40 cm with ca. 15 cm d mesh polyethylene netting overhead, and holes in the fencing to exclude predators while allowing small mammal access;

3) four degu exclusion plots have low (1.0 m h) fencing buried 40 cm without holes to exclude degus while allowing other small mammal and predator access; and,

4) four predator and degu exclusion plots have high (1.8 m h) fencing buried 40 cm and overhead netting, but lacking holes to exclude both predators and degus.

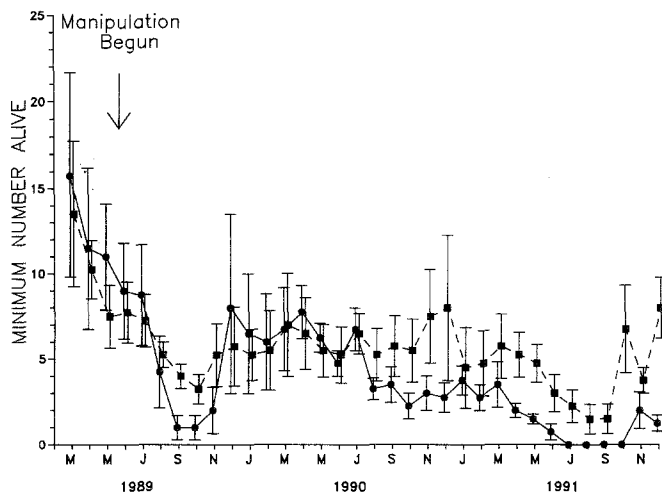
Each of the 16–0.56 ha plots (75 m × 75 m) contains a 5 × 5 array of stations at 15 m intervals which have been trapped for four nights/month since March 1989 with two Sherman-type traps/station using standard mark and recapture techniques. Traps are baited with rolled oats and checked two to three times daily; animals are marked with ear tags or leg bands, and standard data taken on species, number, trap location, weight, sex, reproductive condition, and special remarks. Data from small mammal censuses are analyzed with the CMR (capture-mark-recapture) programs of Le Boulengé (1985).

For purposes of statistical analysis, the experiment is a 2 × 2 factorial design with the factors being degu herbivory (presence or absence) and predation (presence or absence). Only results from control (C) and predator exclusion (-P) treatments will be considered here. 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 and Torrie 1980). However, population trends after assignment but prior to completion of the exclusions dictated pooling of replicates within treatments. Monthly trappability for degus averaged  $66.15 \pm 3.27$  (1SE)%. Minimum number known alive numbers were analyzed using one-way MANOVAs (GLM procedure, SAS, Cary, NC) to identify time effects resulting from interdependency of sequential census data (i.e., repeated measures), and treatment effects (i.e., predator exclusions). Responses to experimental manipulations were analyzed in three month periods corresponding approximately to the major climatic seasons in Fray Jorge; fall (March–May), winter (June–August), spring (September–November), and summer (December–February; also used by Jaksic et al. 1992, 1993). Foxes removed degus from traps on the grids during censuses on 24 occasions; these were added to minimum number known alive numbers for statistical analyses. Since fence construction was completed in May 1989, the first three months (March–May) constitute a pre-test period.

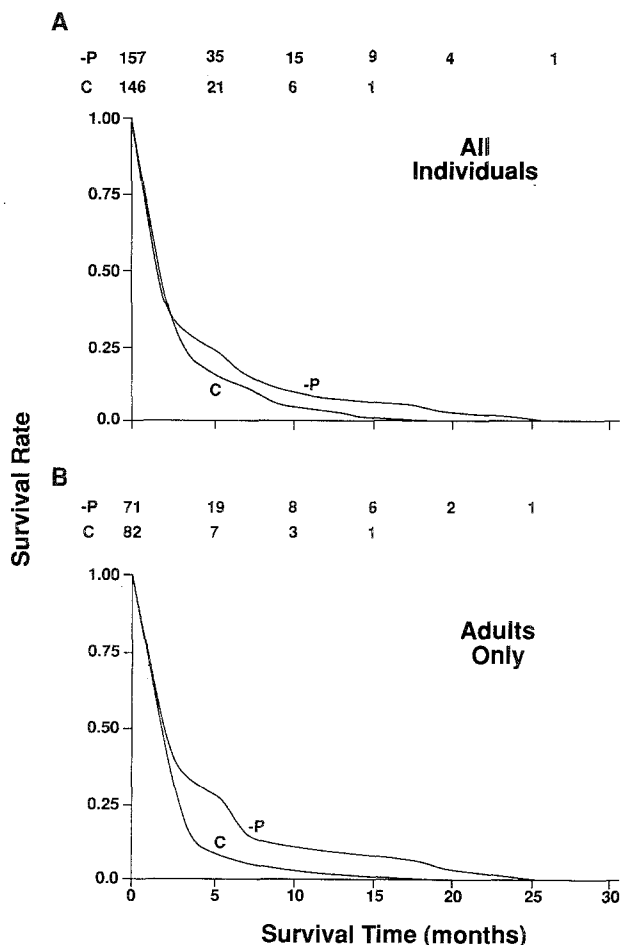
Survivorship of degu was compared for all individuals on control (C) and predator exclusion (-P) grids using the NCSS Survival Analysis package (Kaysville, UT). Trap-revealed persistence times in months of individuals from first to last capture was determined starting in June 1989 (time of experiment initiation); data from individuals with captures after November 1991 were considered right-censored. Distributions of cumulative survival times were found to most closely approximate exponential distributions, and statistical comparisons were made with the Cox-Mantel test which is more powerful for such distributions (Lee 1980). Survival times were also compared between individuals first caught as juveniles or subadults, or as adults. Since degus lack pelage changes after weaning, body weight was used to assign age (Meserve and Le Boulengé 1987); juveniles weighed <90 g, subadults 90–119 g, and adults ≥ 120 g.

## Results

Figure 1 shows minimum number known alive estimates for *Octodon degus* on control (C) and predator exclusion grids (-P) through December 1991. Results of a one-way MANOVA for March–May 1989 (factor = predation;



**Fig. 1.** Mean minimum number known alive trends for degus in Fray Jorge on four control grids (C; solid dots and lines), and four predator exclusion grids (-P; solid squares and dashed lines) during March 1989–December 1991. Arrow indicates when exclusions of terrestrial predators became effective; exclusions of aerial predators was complete by September 1989. Vertical lines and intervals include one standard error of the mean



**Fig. 2.** A Survival rates of all degus on control (C) and predator exclusion (-P) grids between June 1989 and November 1991; numbers of individuals surviving cumulative five month periods are listed across top of graph. B Survival rates of adult degus on control (C) and predator exclusion (-P) grids between June 1989 and November 1991; codes and numbers across top of graph are as in A

intercept-time) showed no differences between treatments prior to the start of the experiment ( $F_{(1,6)}=0.24$ ,  $p=0.64$ ). After initiation of exclusions, the greatest (although nonsignificant) differences were observed in September–November 1989 ( $F_{(1,6)}=3.28$ ,  $p=0.12$ ), and September–November 1990 ( $F_{(1,6)}=2.16$ ,  $p=0.19$ ). Higher mean densities of degus were also observed (Fig. 1); in these months, degu densities on predator exclusion grids averaged  $4.2 \pm 0.7$  (1 SE), and  $6.3 \pm 1.1$  individuals/grid in 1989, and 1990, respectively, vs.  $1.3 \pm 0.5$ , and  $2.9 \pm 0.5$  individuals/grid, respectively, on control grids. Degus disappeared entirely from control grids in 5/12 cases in September–November 1989. From March 1991 on, differences between control and predator exclusion grids became persistent (Fig. 1) and increasingly significant (March–May:  $F_{(1,6)}=3.66$ ,  $p=0.10$ ; June–August:  $F_{(1,6)}=4.34$ ,  $p=0.08$ ; September–November:  $F_{(1,6)}=8.11$ ,  $p=0.029$ ). Degus disappeared from all control grids from July to October 1991.

Degu survivorship differed significantly between treatments for the entire analysis period. A comparison of survival distributions of all individuals showed that they survived significantly longer on predator exclusion grids than on control grids (Cox-Mantel test,  $Z=1.93$ ,  $p=0.05$ ; A, Fig. 2). Out of 146 individuals, only one (0.7%) survived more than 15 months on predator open grids (maximum of 19 months); in contrast, nine (5.7%) out of 157 individuals survived more than 15 months on predator exclusion grids, and maximum survival time was 26 months (A, Fig. 2). A comparison among age groups showed no significant differences between survival times of individuals first caught as juveniles or subadults on control vs. predator exclusion grids (Cox-Mantel test,  $p=0.76$ , and 0.62, respectively). However, individuals first caught as adults had significantly longer survival times on predator exclusion grids ( $Z=2.59$ ,  $p=0.01$ ; B, Fig. 2). Adult degus captured in March–May 1989 prior to the start of the experiment also had significantly longer survival on predator exclusion grids ( $Z=2.65$ ,  $p=0.008$ ) while adults first caught after the start of the experiment had only marginally significant longer survival ( $Z=1.65$ ,  $p=0.099$ ). Thus, exclusion of predators had greater effects on adults than on other age classes of degus, and greater effects on established adults vs. newer (immigrant) adults. There were no statistically significant differences in survival distributions of males vs. females for any age or residency classes (all  $p>0.20$ ).

Dietary analyses during 1989–1991 showed that owls preyed primarily on non-degu species and that foxes (*Pseudalopex culpaeus*) utilized degus and *Abrocoma benetti* disproportionately ( $\chi^2$  test,  $p<0.001$ ; Jaksic et al. in press); observations and radio-tracking verified the presence of five to seven foxes in the vicinity of the study area during early-mid 1991. This number decreased to two-three foxes in November–December 1991.

## Discussion

The results here indicate that exclusion of predators can have temporally varying effects on a primary prey species. In degus, through the first two years, exclusion of culpeo foxes resulted in strongest (but nonsignificant) effects during spring months (September–November), when numbers of degus were seasonally low (Fig. 1). Following this period, degu populations recovered to similar levels during December–February 1989–90, and 1990–91. This recovery was due to *in situ* reproduction and recruitment, and immigration into the trappable population which was sufficient to compensate for predation losses.

After March 1991, differences between numbers of degus in control and predator exclusion grids became persistent and increasingly significant. Thus, effects of predators became more pervasive during a period when small mammal populations including degus were declining generally (Fig. 1; Meserve et al. 1993). Similar to some other studies, predation appears to have greater effects when prey populations are low (e.g., Pearson 1966, 1971, 1975; Lidicker 1973; Newsome et al. 1989; Sinclair et al. 1990; Arçakaya 1992). Erlinge et al. (1983, 1984, 1988) and Hanski et al. (1991) emphasize the importance of generalist predators in damping oscillations in prey populations. However, most of these studies emphasize the importance of such effects in small mammals with multiyear cycles. Here, in the annually cyclic degu, such effects may be seasonal until a general decline occurs such as in 1991 when effects become more pervasive.

Despite these temporally varying effects, survival times of adults were longer on predator exclusion grids; juveniles and subadults did not show significantly different survival distributions. Thus, there were greater consequences of predator exclusions for adult degu survival. The poorer survival of adult degus on control grids may reflect positive size selection for larger individuals by foxes. As a result, once protected from predators, adult survival times increase. This effect was particularly strong for adults previously established on the plots prior to the experiment initiation. Thus, residency status may also be important in the differential effects of predators on this highly social, diurnal species (Fulk 1976b; Yáñez and Jaksic 1979; Meserve et al. 1984). Ultimately, established adults in predator exclusion grids could influence deme age composition and social structure with significant consequences for the breeding and genetic structure. They also may contribute more to the reproductive effort of the local population by virtue of their longer lifespans and greater opportunities to breed in predator exclusion grids. Thus, predators have potentially strong effects on their prey at the individual level as well as overall numerical effects.

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