A Long-Term Study of Vertebrate Predator Responses to an El Niño (ENSO) Disturbance in Western South America

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A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America

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We analyzed the putative effects of the El Niño Southern Oscillation (ENSO) of 1991–92 in a semi-arid locality of northern Chile. We obtained 30 months of pre-ENSO data, followed by 36 months of peak and post-ENSO data (total = 5.5 yr). The rainy winter of 1991 resulted in a three-fold increase in total seed bank (perennial and ephemerals pooled) and in ephemeral (but not perennial) herb cover. Seed and herbage eaters (rodents) irrupted to population levels ca 20 times higher during the breeding season of 1991 than the preceding wintering season. Diurnal carnivorous predators (hawks, owls, and foxes) showed a delayed response to the irruption, increasing from seven individuals sighted during the wintering season of 1991 to 13 during the wintering season of 1992. A seemingly counterclockwise trajectory of predator abundance versus prey levels suggested a pattern of prey-driven dynamics, but confidence intervals were likely broad. In this semiarid locality, it appears that ENSO effects did not cascade down from higher to lower trophic levels, but rather the opposite. In this bottom-up scenario, we predict that as primary productivity varies with rainfall, so should secondary (mammal prey densities), and tertiary productivity (vertebrate predators). Long-term monitoring of this terrestrial ecosystem is needed to test this prediction.

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The El Niño Southern Oscillation (ENSO) is an hemispheric-scale phenomenon that originates off the northeastern coast of Australia, and causes multiple effects across the Pacific Ocean on the western coastline of the Americas (Diaz and Markgraf 1992). Although generally studied in atmospheric and oceanographic contexts, some associated biological phenomena have been reported (Barber and Chavez 1983), particularly geographic and bathymetric shifts in marine life, including marine birds (e.g., Guerra et al. 1988), and more sporadically, changes in terrestrial floral composition (e.g., Dillon and Rundel 1990, Villagrán 1993). ENSO effects on terrestrial fauna have long been suspected, but poorly documented.

Among those putative effects, outbreaks (or irruptions, "ratadas") of small mammals have frequently been reported in association with ENSO disturbances in semi-arid regions of western South America (Hershkovitz 1962). Several researchers noted the mammal outbreaks that occurred in southern Peru and north-central Chile (Table 1). All of them concurred that these outbreaks were triggered by unusually high rainfall (Table 1). Indeed, Fuentes and Campusano (1985) found an overall significant association between high rainfall years and mammal outbreaks throughout north-central Chile. The mechanism linking these two phenomena appears to be increased primary productivity, both as herbage production and seed

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Table 1. Mammal outbreaks and rainfall patterns in western South America.

Place and date of outbreak	Chief mammal respondent	Year's rainfall	Mean yearly rainfall	Previous year rainfall	Authority
Coastal Peru, 1972	*Phyllotis darwini*	81 mm	32 mm	no data	Pearson (1975)
Fray Jorge, Chile, 1972	*Phyllotis darwini*, *Akodon olivaceus*	255 mm	69 mm	72 mm	Fulk (1975), Meserve and Le Boulengé (1987)
La Serena, Chile, 1972	*Oligoryzomys longicaudatus*	174 mm	82 mm	80 mm	Péfaur et al. (1979)
Aucó, Chile, 1987	*Phyllotis darwini*, *Akodon olivaceus*, *Thylamys elegans*	513 mm	206 mm	158 mm	Jiménez et al. (1992)
Fray Jorge, Chile, 1991	*Phyllotis darwini*, *Akodon olivaceus*, *Octodon degus*	233 mm	85 mm	32 mm	Meserve et al. (1995)

bank storage (Armesto et al. 1993, Gutiérrez et al. 1993a, b).

Here we scrutinize the long-term database accumulated in Fray Jorge (north-central Chile), for primary production and small mammal abundance, and analyze the putative effects of the 1991–92 ENSO disturbance on the higher trophic level, that of vertebrate predators. The theoretical framework of our study refers to three major components of vertebrate predation: numerical, functional, and guild responses shown by predators when faced with fluctuating mammalian prey populations. When prey abundance increases, predators may respond numerically by immigrating from peripheral areas and (or) reproducing more successfully in situ (Solomon 1949). When prey abundance declines, predators may decrease by emigrating, failing to reproduce, or dying. Functional responses, on the other hand, involve changes in the relative numbers of prey eaten by individual predators as prey densities vary (Holling 1959). Here, we are interested in a particular expression of functional response, the prey switching behavior of predators (Murdoch 1969, Murdoch and Oaten 1975), whereby they change their selection of prey depending on the relative frequency that prey are encountered in the field. The third component refers to the trophic guild structure of predators (Marti et al. 1993). In this case, we are interested in assessing whether guild composition and packing differs between pre- and post-ENSO changes in prey levels. We test whether numerical, functional, and/or guild responses are displayed by predators faced with fluctuating prey resources brought by the 1991–92 ENSO disturbance at Fray Jorge.

Study site and methods

Study site

The study site is located in a semi-arid mediterranean scrub community in Quebrada de las Vacas (240 m elevation), an interior valley in Fray Jorge National Park (30°38′S, 71°40′W), north-central Chile. This low elevation scrub zone contains a homogeneous cover of spiny drought-deciduous and evergreen shrubs, and a herbaceous understory, on a predominantly sandy substratum. The most characteristic plant association is that of *Porlieria chilensis – Proustia pungens – Adesmia bedwellii* (Muñoz and Pisano 1947), with mean shrub cover averaging 59% (Meserve 1981a, b). The semi-arid mediterranean climate of this site has 90% of the mean 85 mm annual precipitation falling between May and September (from late autumn to early spring in the southern hemisphere), and warm, dry summers.

Prey abundance

Since May 1989, a large scale experimental manipulation has been in progress at the study area, involving the selective exclusion of vertebrate predators and (or) large-sized small mammal herbivores from 16 fenced 75 by 75 m (0.56 ha) plots. Small mammal populations are being monitored on all plots with grids consisting of 5 rows by 5 columns (i.e., 25 stations at 15-m intervals) trapped for 4 d/month with two Sherman-type live traps/station. Standard mark and release techniques (Meserve and Le Boulengé 1987) are used with data taken on small mammal species, number, trap station, sex, reproductive condition, and weight. Meserve et al. (1993a, 1996) provide full details on the rationale and layout of the experimental setup.

For the purposes of this report, small mammal abundance was determined from monthly live-trapping in the four control grids open to both predators and small mammal species (potential prey). Determinations of minimum number known alive (MNKA) were obtained using the CMR capture-recapture program (Le Boulengé 1985, Meserve and Le Boulengé 1987). Trappability was high (>90%) for most species, enabling use of enumeration techniques. Monthly MNKA estimates on the four control grids were averaged together and then averaged again for the six-month periods corresponding to two major biological seasons: breeding season (September–February) and wintering season (March–August), for generation of "expected" frequencies of small mammals in predator diets (see Jaksic et al. 1993a and below).

Predator abundance

Starting March 1989 (wintering season), a quantitative estimate of the abundance of diurnal predators (seven hawks, one diurnal owl, one fox species) was obtained by recording the number of different individuals observed daily at the study site. Three nocturnal owl species were monitored by collecting their regurgitated pellets and – starting in early 1990 – by their calls, which only allowed records of their presence/absence. Approximately 750 ha in the vicinity of the trapping grids in Quebrada de las Vacas were covered by this tally, conducted simultaneously with the trapping sessions (i.e., 4 d/month).

Predator food habits

Fresh raptor pellets and fox feces were collected on a monthly basis starting March 1989 (wintering season). Regurgitated pellets of both diurnal and nocturnal raptors were collected under known roosts, nests, or perches in a 750-ha area approximately centered in the trapping grid area. Feces of foxes were collected in and around trapping grids (see below). Prey were identified with a dissecting scope, usually to the species level, using keys (Reise 1973) and locally collected voucher specimens. The minimum number of individual prey items in pellets and feces was estimated on the basis of paired or unique anatomical elements such as crania, mandibles, teeth rows, wings, elytra, antennae, stings, etc. (Marti 1987). Because all local predators fed on vertebrates and large arthropods (see below), we assume that our tabulations are essentially complete representations of predator diets.

Predator numerical response

Because we obtained data on the temporal course of small mammal population numbers, we can assess the numerical response of local mammal-eating predators to changes in those prey levels. The non-parametric Spearman coefficient was used to assess the degree of correlation between those two variables (Siegel and Castellan 1988).

Predator selectivity

Chi-square goodness-of-fit tests were run between observed frequencies of small mammals in predator diets, and the expected frequencies generated from trapping data (cf. Pearre 1982, Jaksic 1989a). Small mammal species were pooled whenever necessary to obtain expected frequencies >5, as required by the Chi-square test (Sokal and Rohlf 1981). When a given mammal species appears in a predator's diet more than expected from its field abundance as estimated by trapping, we say that this prey species is "selected", meaning that it is overrepresented in the predator's diet. Similarly, a prey is "underconsumed" (we prefer not to imply that it is "avoided") when it is found underrepresented in a given predator's diet.

Predator selectivity was assessed on a biological-season basis (i.e., 6-month periods). To take advantage of the long-term aspect of our study, we analyzed these selectivity data as a time series. Departures between prey frequencies in diets and in the field could go either way, from overrepresentation (positive departure = selectivity) to underrepresentation (negative departure). The time series was analyzed in terms of the sign of the departures by means of the binomial test (Siegel and Castellan 1988). The series was examined even when yielding non-significant values, searching for interesting patterns such as selectivity before or after the small mammal irruption that occurred during the breeding season of 1991. We did this because a short series of positive values followed by one of negative values (or the reverse) yields a statistically non-significant result with the binomial test, but is suggestive of a prey selectivity shift on the part of the predators.

Predator guild structure

We computed diet overlap between any two predator species (cf. Marti 1987) as:

$$\mathrm{Ov} = \sum p_i q_i \Big/ \left(\sum p_i^2 \sum q_i^2 \right)^{1/2},$$

where p_i and q_i are the relative occurrences of prey category i in the diets of the two predators, respectively. Ov ranges from 0 to 1 (0–100% overlap). We applied this equation to diet data using the highest possible taxonomic resolution of prey (plant foods were not considered): species for vertebrates and orders for invertebrates (cf. Greene and Jaksic 1983). Using entries in the diet similarity matrices constructed for calculating Ov, we applied the unweighted pair-group clustering method with arithmetic averaging (UPGMA, Sneath and Sokal 1973). Following Marti et al. (1993) and in order to compare results from throughout the study period, we set the threshold for assigning predators to trophic guilds at 50% diet similarity. Less arbitrary means of defining guilds (e.g., Jaksic and Medel 1990) would result in thresholds for guild designations that varied seasonally, rendering comparisons of guild structure between seasons and among years much more difficult (Jaksic et al. 1993b). Statistical comparisons between the levels at which guild nodes (branches) formed during pre- and post-ENSO years were made with the Mann-Whitney U test (Siegel and Castellan 1988, see Jaksic et al. 1993b for a similar approach).

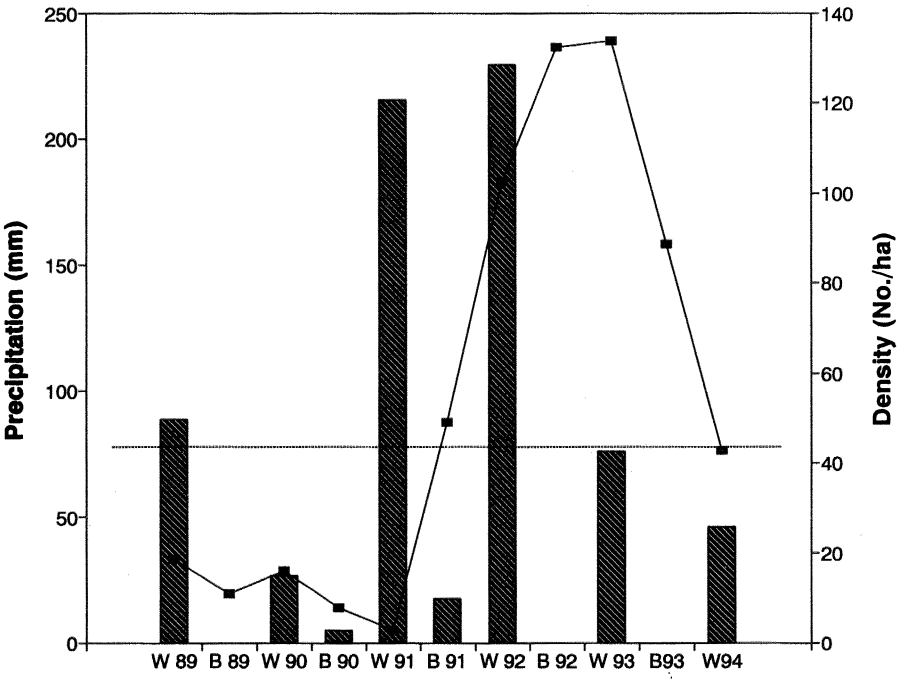

Fig. 1. Seasonal precipitation and small mammal density ($n = 6$ months/season) at Fray Jorge National Park, north-central Chile, throughout 11 successive biological seasons (W = wintering season, March through August; B = Breeding season, September through February). The horizontal line indicates the most recent 10-yr average (85 mm).

Results

Prey abundance

Total abundance of small mammals was positively associated with rainfall (Fig. 1). They were apparently declining from the wintering season of 1989 and reached their lowest abundance in the wintering season of 1991. That season, rainfall exceeded 200 mm, and small mammal abundance during the breeding season of 1991 increased to almost 20 times their previous abundance. They continued increasing until the wintering season of 1993, and started declining again, reaching during the wintering season of 1994 an abundance level similar as that observed during the breeding season of 1991. That a lag existed between winter rainfall pulses and population responses may be related to the fact that local small mammals start reproducing during early spring (Fulk 1976, Meserve and Le Boulengé 1987).

Seven species of small mammals (six rodents, one marsupial) were captured throughout the study period (Table 2). *Octodon degus*, *Phyllotis darwini*, and *Akodon olivaceus* were the most abundant species at the site. They accounted for an overall 36%, 24%, and 23% of small mammal captures, respectively, and were present throughout the study (Table 2). The remaining four species together accounted for only 17% of total captures. Of these, *Abrocoma bennetti*, *Abrothrix longipilis*, and *Oligoryzomys longicaudatus* were not captured at all during entire seasons. The only marsupial, *Thylamys elegans*, although never abundant, was present throughout the study period.

Predator abundance

The most abundant diurnal raptors were the black-chested eagle (*Geranoaetus melanoleucus*) and the Chimango caracara (*Milvago chimango*). These two species were observed flying over (but infrequently perching) during virtually all seasons (Table 3). Harris hawks (*Parabuteo unicinctus*), red-backed hawks (*Buteo polyosoma*), and American kestrels (*Falco sparverius*) were less frequently observed flying over the study site, and seldom perching. They were absent from the study site during whole seasons. The remaining diurnal raptors, peregrine falcon (*Falco peregrinus*) and Aplomado falcon (*Falco femoralis*), were of sporadic occurrence at the study site, each sighted only during a few seasons.

Four species of owls were detected at the study site, but only the diurnal burrowing owl (*Speotyto cunicularia*) could be censused (Table 3). The nocturnal great horned owl (*Bubo virginianus*) and barn owl (*Tyto alba*) were heard, and their pellets were collected through all seasons in the field (see below). The pygmy owl (*Glaucidium nanum*) was frequently heard but their pellets were not found in all seasons (see below). Despite Fulk's (1976) report, we did not see or hear short-eared owls (*Asio flammeus*) at the study site.

Only one species of mammalian carnivore was observed at the study site (Table 3), the Culpeo fox (*Pseudalopex culpaeus*). Reptilian predators were sporadically seen and consisted of only the long-tailed snake (*Philodryas chamissonis*) and the Chilean racerunner (*Callopistes palluma*), both diurnally active during summers.

Table 2. Small mammals trapped at Fray Jorge National Park, north-central Chile. Density (number/ha) and percentage of total sample that season came from estimates of minimum number known to be alive. Tabular entries are means of six monthly assessments made in four 0.56-ha live-trapping grids. W = wintering season (March through August), B = Breeding season (September through February).

Species	W89	B89	W90	B90	W91	B91	W92	B92	W93	B93	W94	Mean ($n = 11$)
Abrocoma bennetti	1.1	0.0	1.3	4.8	1.5	0.6	0.1	1.1	1.3	2.6	1.2	1.4
Abrothrix longipilis	8.7	4.9	2.6	0.0	0.0	4.2	8.1	8.5	9.6	11.3	11.1	6.3
Akodon olivaceus	14.5	14.0	11.6	4.8	6.1	60.6	44.1	45.6	28.1	14.4	9.7	23.0
Octodon degus	53.0	37.1	36.7	38.5	47.0	3.2	5.9	20.3	34.5	46.2	70.5	35.7
Oligoryzomys longicaudatus	0.2	5.3	10.6	0.0	0.0	8.9	18.8	1.3	1.0	0.8	0.0	4.3
Phyllotis darwini	20.3	26.5	29.5	44.4	33.3	19.2	19.3	21.9	24.2	22.6	3.9	24.1
Thylamys elegans	2.2	12.1	7.8	7.5	12.1	3.4	3.6	1.3	1.2	2.1	3.7	5.2
Density (No./ha)	18.7	11.0	16.1	7.8	2.8	49.1	102.5	132.3	133.8	88.6	43.0	55.1

Predator numerical response

As shown below, the four owl and one fox species studied at the site are generally mammal eaters. Although we did not collect dietary data on the remaining predators, results obtained over seven years at the nearby site of Aucó indicate that the Harris hawk (63–100% of numerical prey occurrences), red-tailed hawk (41–70%), black-chested eagle (33–63%), and American kestrel (0–17%) are mostly to partially mammal-eaters (Jaksic et al. 1996). Chilean racerunners in Aucó are essentially insectivorous (84% of its diet by numbers), with mammals comprising only 9% of prey occurrences over one year of study (Castro et al. 1991). However, they may sometimes prey extensively on small rodents (Mellado 1982). Also at Aucó, Aplomado falcon was reported to prey mostly on birds and not at all on mammals over one breeding season (Jiménez 1993). Chimango caracaras from Pudahuel preyed mostly on insects (87% of its diet by number) and rarely (2%) on mammals (Yáñez et al. 1982), but their biomass contribution was not that negligible. Long-tailed snakes from all over Chile have been reported (Greene and Jaksic 1992) to prey mainly on reptiles and amphibians (80% by number), and less on mammals (12%). The only predator present in Fray Jorge for which there are no dietary data is the peregrine falcon, likely a bird-eater (Jaksic, pers. obs.).

In summary, all predators present at our study site (except for two of the three falcons) depend to some extent on mammal prey. Therefore, disregarding both peregrine and Aplomado falcons, we pooled our seasonal censuses of predators, and evaluated whether they collectively varied in numbers together with their presumed prey resources. Fig. 2 indicates that this was the case. Early during the study, predators were declining, in phase with decreasing mammal densities. The irruption during the breeding season of 1991 apparently fueled an increase in the number of predator individuals sighted at the site (Fig. 2). Their increase lasted until the wintering season of 1993, when they abruptly declined together with their main prey. At the end of our study (wintering season of 1994), predator abundance was similar to that observed in the beginning. A seemingly counterclockwise trajectory of predator abundance in association to varying prey levels suggests a prey-driven dynamics (Jaksic et al. 1996). Nevertheless, the confidence intervals associated with estimates of both predator and prey abundance are unknown and likely broad, thus rendering this conclusion rather speculative. Spearman's r was 0.738 ($n = 11$, $P = 0.0095$).

Predator food habits

Overall, 4672 pellets and 2180 feces were collected, and 16 660 prey items were identified. The presence of plant material (mostly fruit seeds) in fox feces was also observed (cf. Castro et al. 1994). Pellets of the four owls were collected, but only those of great horned owls, barn owls, and burrowing owls were found in all seasons. Pellets of pygmy owls were less frequent, and those of diurnal raptors were found only exceptionally. Our observations indicate that the owls exhibited a much higher site fidelity than the wide ranging diurnal raptors. The roosting and nesting sites of local owls were all within 4 km of the trapping grids. Roosting and nesting sites of diurnal raptors were located at longer distances from the study site, thus accounting for the scarcity of pellets found. Foxes provided consistent seasonal numbers of feces. No effort was made to collect feces of either long-tailed snakes or Chilean racerunners.

Great horned owls ate primarily mammals (63–100% of prey occurrences throughout the study period; Table 4). Insects and arachnids occurred at widely fluctuating levels in the diet (combined figures ranged between 0–36% by numbers); much of the invertebrate consumption may be due to juvenile owls (Jaksic, pers. obs.), which appear to be indiscriminate predators as they develop their hunting skills. Birds were consistently consumed at low levels, whereas reptiles and amphibians were only rarely taken.

Barn owls preyed mainly on small mammals (56–100% of their prey throughout the study; Table 4).

Table 3. Mean number/season ($n = 6$ months) of vertebrate predator individuals sighted at Fray Jorge National Park, north-central Chile, throughout 11 biological seasons (wintering and breeding). Area surveyed was 750 ha. ns = not seen but heard, nh = neither seen or heard.

Species	W89	B89	W90	B90	W91	B91	W92	B92	W93	B93	W94	Mean ($n = 11$)
Falconiforms (hawks)												
Buteo polyosoma	1.0	1.0	0.0	0.2	0.0	0.3	1.0	3.2	1.7	1.5	1.0	1.0
*Falco femoralis**	0.0	0.0	1.0	0.0	0.0	0.0	0.2	0.5	0.7	0.5	0.0	0.3
*Falco peregrinus**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.0	0.5	1.5	0.3
Falco sparverius	1.0	1.0	1.0	1.0	0.3	0.2	1.2	1.7	1.2	1.2	0.3	0.9
Geranoaetus melanoleucus	2.0	2.0	3.0	2.3	1.3	1.7	3.2	3.3	3.7	1.7	2.7	2.4
Milvago chimango	2.0	2.0	3.0	1.5	0.2	1.0	1.5	2.7	2.8	2.7	1.7	1.9
Parabuteo unicintus	1.0	1.0	1.0	0.5	0.2	0.2	1.2	1.3	3.5	1.5	2.3	1.2
Strigiforms (owls)												
Speotyto cunicularia	2.0	2.0	2.0	2.8	2.2	2.0	3.0	6.0	6.8	2.0	2.7	3.0
Bubo virginianus	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–
Glaucidium nanum	nh	nh	nh	ns	ns	ns	ns	ns	ns	ns	ns	–
Tyto alba	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–
Carnivores (foxes)												
Pseudalopex culpaeus	2.0	2.0	2.0	1.7	2.8	0.7	1.8	1.3	1.0	1.0	1.7	1.6
Total (No./750 ha)	11.0	11.0	13.0	10.0	7.0	6.0	13.0	20.2	22.3	12.5	13.8	12.7

* Not considered in Fig. 2 because it is a bird-eater.

Insects and arachnids fluctuated widely in the diet (combined figures 0–40%). Birds were consistently taken at low numbers, but not reptiles or amphibians.

Burrowing owls ate primarily insects and arachnids (combined figures 51–96% throughout the study period; Table 4), but also mammals (2–49%). The biomass contribution of mammals, however, was much higher than that of invertebrates (Silva et al. 1995). Birds and reptiles were rarely preyed upon, whereas amphibians were more prevalent in their diet. These amphibians were all terrestrial toads (*Bufo chilensis*), and were only partly consumed, as burrowing owls discarded the intestines and the apparently distasteful integument.

Pygmy owls generally ate more mammals (13–100% of prey occurrences throughout the study; Table 4) and fewer insects (0–76%) than did burrowing owls. The former also ate more non-mammalian vertebrates, specifically birds. Neither amphibians nor reptiles (except for a single snake) were found in the diet of pygmy owls.

Culpeo foxes ate primarily mammals, but with large fluctuations (12–98% of prey occurrences throughout the study; Table 4). Insects and arachnids together comprised from 0 to 79% of prey occurrences, in keeping with reverse trends of mammal consumption. Birds and reptiles were consistently preyed upon (though not amphibians), but their combined occurrences never exceeded 19%. Fruit seeds were frequent in the feces only during the breeding season of 1990 and the wintering season of 1991. Castro et al. (1994) reported that Culpeo foxes in Fray Jorge ate fruits only when mammal abundances were very low, which was clearly the case during those two seasons (Fig. 1, Table 4).

Predator selectivity

Great horned owls significantly selected *O. degus* (i.e., took it in higher proportion than expected) and underconsumed both *A. longipilis* and *A. olivaceus* (Table 5). A selectivity shift away from *P. darwini* became evident after the breeding season of 1991. Barn owls selected *P. darwini* with a marginally non-significant probability ($P = 0.066$) and significantly underconsumed *A. longipilis*, *A. olivaceus*, and *O. degus* (Table 5). They apparently selected *A. bennetti* early in the study but generally ignored it after the breeding season of 1991. Burrowing owls significantly selected *P. darwini* and underconsumed *O. degus* throughout the study (Table 5). Both *A. longipilis* and *A. olivaceus* appeared to be selected prior to the breeding season of 1991 and were consistently ignored afterwards. Pygmy owls showed no significant preference for any small mammal, but they significantly underconsumed both *T. elegans* and *O. degus* (Table 5). It should be noted that in the case of this owl, the time series was shorter than for all other owls (six vs eleven seasons, respectively). This renders it more difficult to detect significant departures. Likely, pygmy owls did select *P. darwini* and underconsumed *A. bennetti*. Culpeo foxes significantly selected *A. bennetti* (Table 5), whereas they underconsumed *A. longipilis*, *A. olivaceus*, and *T. elegans* throughout the study (note that they also underconsumed *P. darwini* at a marginally non-significant level; $P = 0.066$). Culpeo foxes appeared to select *O. degus* after the breeding season of 1991, when small mammals irrupted in association with the ENSO disturbance.

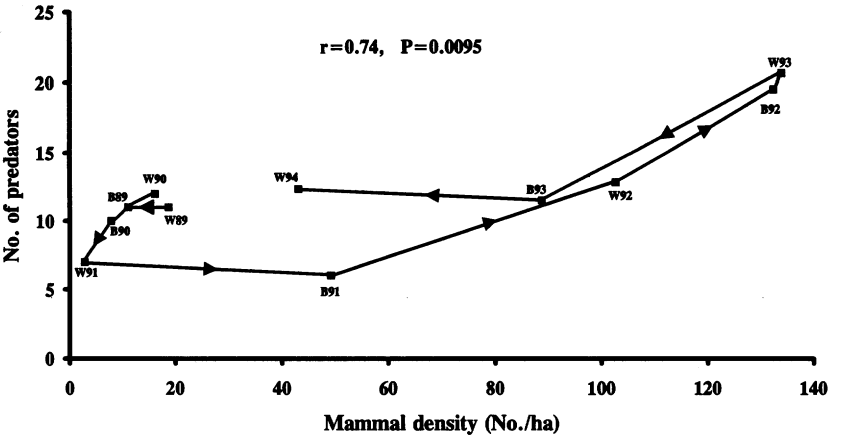

Fig. 2. Numerical response of mammal-eating vertebrate predators to small mammal densities at Fray Jorge National Park, north-central Chile, throughout 11 successive biological seasons (wintering and breeding).

Predator guild structure

Before the ENSO disturbance (up to the wintering season of 1991), the following trophic guild structure was observed. Great horned and barn owls formed a tight mammal-eating guild during the first five seasons of the study (Fig. 3). These two owls clustered together because of their high and shared consumption of *P. darwini* and *A. bennetti*. The burrowing owl clustered with the Culpeo fox alone during one season, with both the Culpeo fox and pygmy owl during one, with all three predators during another, and kept separate during the remaining two seasons. Shared insectivory (in addition to carnivory) among the burrowing owl, Culpeo fox, and pygmy owl accounted for their frequent association in an omnivorous guild.

The breeding season of 1991, with the onset of the mammal irruption brought together again the burrowing owl, Culpeo fox, and pygmy owl into a close omnivorous guild, and once again, great horned and barn owls remained in a tight mammal-eating guild which concentrated on *P. darwini* and *A. bennetti* as prey.

From the wintering season of 1992 on, an interesting reshuffling of guild membership occurred (Fig. 3). The great horned owl clustered with the Culpeo fox during all of the five seasons considered, owing to their high and shared consumption of *A. bennetti* and *P. darwini*. The barn owl continued preying substantially on these same two prey species during the wintering season of 1992 and thus joined both the great horned owl and the Culpeo fox. Staring in the breeding season of 1992, however, the barn owl shifted from preying on *A. bennetti* toward *A. olivaceus*, and disengaged from those two predators. Because the burrowing and pygmy owls, in addition to insects, also preyed on *P. darwini* and *A. olivaceus*, they now clustered more closely with the barn owl. Only during the last season of the study (wintering season of 1994) did the barn owl converge again toward the great horned owl and Culpeo fox, because of its increased consumption of *A. bennetti*.

The levels of similarity at which guilds formed did not vary pre- or post-ENSO. The 16 guild nodes observed up to the wintering season of 1991 did not significantly differ from the 23 nodes observed later on (Mann-Whitney U test, Normal approximation with continuity correction, $z = 0.071$, $P = 0.943$).

ENSO effects on trophic level productivity

The following aspects of trophic level productivity were observed before, during, and after the 1991–92 ENSO disturbance in Fray Jorge (Table 6). The two pre-ENSO years (1989 and 1990) had average or low rainfall; during 1991 and 1992 rainfall was almost three times the average (85 mm); the two post-ENSO years were similar to 1989 and 1990, respectively.

Primary productivity (Gutiérrez et al. unpubl.) showed the following associations with the rainfall pattern just described (Table 6): The number of perennial species increased only slightly during and after the ENSO disturbance, and their percentage ground cover remained almost constant throughout six years. In contrast, the number of ephemeral species doubled during the ENSO years, and their cover peaked dramatically during 1991, thereafter decreasing to figures similar to pre-ENSO years. The seed bank of perennials peaked in 1991 at about four times the pre-ENSO densities, and thereafter has remained relatively constant at 14 000 seeds/m^2, still about three times higher than during pre-ENSO years. The seed bank of ephemerals peaked in 1992 but only to 50% of previous levels, and then quickly decreased to seed densities even lower than pre-ENSO years.

Secondary productivity, at least that of mammalian seed and herbage eaters (Table 6) in general showed a 1-yr delayed response to the above pulses in primary productivity. Densities of small mammals peaked in 1992 and 1993 at about 6 times those recorded in the previous three years, and then quickly declined to a third that peak in 1994.

Table 4. Diets of predators at Fray Jorge National Park, north-central Chile, by percent of total prey found in pellets or feces throughout 11 biological seasons (wintering and breeding). np = no pellets were found.

Species	W89	B89	W90	B90	W91	B91	W92	B92	W93	B93	W94	Total
Great horned owl												
Mammals	93.9	72.4	86.6	76.9	62.7	89.8	79.8	94.2	96.5	100.0	100.0	1756
Other vertebrates	1.6	1.7	3.0	1.8	0.9	3.1	2.9	5.8	0.9	0.0	0.0	36
Invertebrates	4.5	25.9	10.4	21.3	36.4	7.1	17.3	0.0	2.6	0.0	0.0	288
Number of prey	311	352	202	441	110	98	104	52	114	154	142	2080
Number of pellets	221	222	169	271	63	67	52	34	88	140	142	1469
Barn owl												
Mammals	81.9	55.9	87.6	94.6	77.3	90.2	90.6	99.6	100.0	98.6	100.0	2000
Other vertebrates	7.4	3.7	1.4	2.7	4.5	5.9	1.3	0.4	0.0	1.4	0.0	27
Invertebrates	10.6	40.4	11.0	2.7	18.2	3.9	8.1	0.0	0.0	0.0	0.0	117
Number of prey	94	161	145	37	22	51	234	223	853	219	105	2144
Number of pellets	75	88	117	28	12	39	166	170	633	190	98	1616
Burrowing owl												
Mammals	8.5	3.1	2.9	3.8	2.2	5.7	29.2	38.9	48.6	27.5	10.7	873
Other vertebrates	0.6	4.0	7.2	1.6	1.5	4.2	0.4	0.0	0.0	0.0	0.1	160
Invertebrates	90.9	92.9	89.9	94.5	96.3	90.1	70.4	61.1	51.4	72.5	89.2	7255
Number of prey	839	844	887	1612	1202	262	273	393	292	546	1138	8288
Number of pellets	150	174	207	173	82	32	58	144	138	161	189	1508
Pygmy owl												
Mammals	np	np	np	np	13.2	28.6	58.3	66.7	92.1	100	np	79
Other vertebrates	np	np	np	np	10.5	7.1	0.0	0.0	2.6	0	np	6
Invertebrates	np	np	np	np	76.3	64.3	41.7	33.3	5.3	0	np	53
Number of prey	np	np	np	np	38	14	24	9	38	15	np	138
Number of pellets	0	0	0	0	8	5	14	6	35	11	0	79
Culpeo fox												
Mammals	83.6	12.4	56.4	54.0	43.6	33.2	87.4	90.6	97.9	96.0	93.6	2152
Other vertebrates	7.6	8.6	9.5	11.2	10.7	18.6	5.5	8.3	2.1	2.9	3.7	405
Invertebrates	8.8	79.0	34.1	34.7	45.7	48.2	7.1	1.1	0.0	1.1	2.8	1453
Number of prey	171	614	305	659	692	585	183	372	146	174	109	4010
Number of feces	209	145	235	293	378	178	126	258	119	143	96	2180
Feces with fruits	0.0	0.0	0.0	15.0	64.4	1.8	0.0	0.0	0.0	0.0	0.0	81

Tertiary productivity, that of vertebrate predators, also showed a somewhat delayed response to mammal prey densities (Table 6), declining from 11 and 12/750 ha during pre-ENSO years to only 7 during 1991, when small mammals began increasing. When the mammal irruption was in full swing (1992 and 1993), predator densities reached a peak of 17/750 ha during both years, and decreased slightly as mammal populations crashed the following year. Note that we could not assess the numbers of nocturnal owls at the site, but they likely followed the same pattern.

Discussion

Changes in mammalian prey abundance

With overall densities ranging from a low of 3 individuals/ha during the wintering season of 1991 to a high of 134 during the wintering season of 1993, there were also marked changes in the composition of the mammalian assemblage (see also Meserve et al. 1995). Before the ENSO disturbance (up to the wintering season of 1991), *O. degus* was proportionally stable, *P. darwini* was increasing, and *A. olivaceus* was decreasing. Afterwards, *A. olivaceus* irrupted markedly but briefly, whereas *O. degus* picked up slowly but steadily reaching 71% of all captures by the end of the study. *P. darwini* hovered at about 20%, except at the very end when it reached a low of 4% of all captures. This inconstancy in relative abundance of mammalian prey thus provides a crucial cue for changing the predators' search image, and hence facilitate prey switching (Murdoch 1969, Murdoch and Oaten 1975). Over the entire span of the study and from the viewpoint of predators, *O. degus* was increasing in the field, *P. darwini* was a relatively predictable prey, and *A. olivaceus* was an irruptive species.

Numerical response of predators

Ten predator species were year-round residents at the study site (five hawks, four owls, and one fox). They responded numerically to mammalian prey levels, but we could not determine if they did so by immigrating into the area after the ENSO disturbance, by reproducing more successfully in situ, or both. The burrowing owl was the predator that most strongly responded to mammalian increases, which indicates that although insects numerically dominate its diet, mammals are its staple prey (Silva et al. 1995).

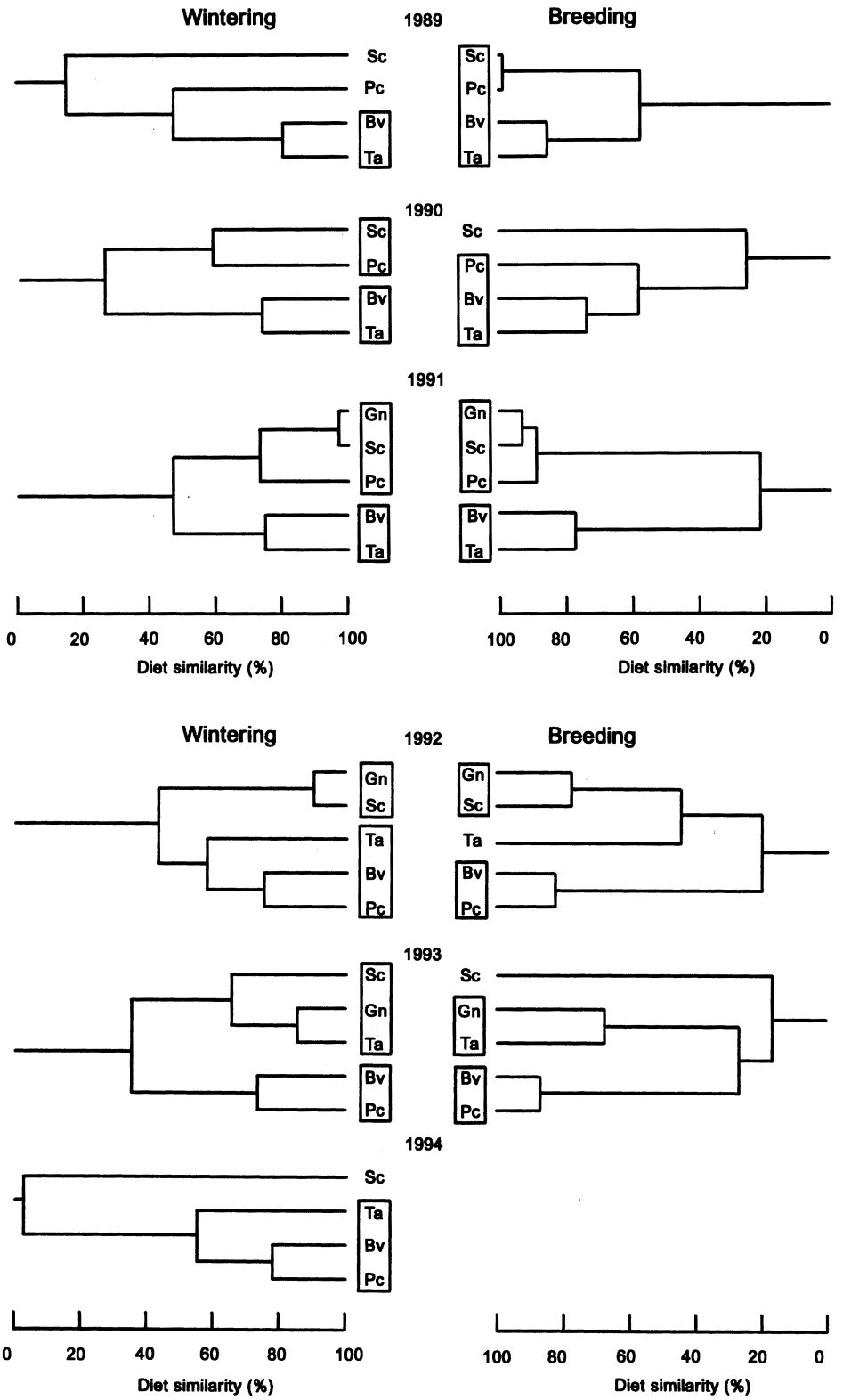

Fig. 3. Trophic guild structure of predators at Fray Jorge National Park, north-central Chile, throughout 11 biological seasons (wintering and breeding). Diet similarities close to 100% indicate high overlaps in diet; those close to 0% indicate distinct diets. Trophic guilds recognized are those with >50% diet similarity (species encased in boxes). Species abbreviations are: Bv, *Bubo virginianus*; Ta, *Tyto alba*; Pc, *Pseudalopex culpaeus*; Gn, *Glaucidium nanum*; and Sc, *Speotyto cunicularia*.

Table 5. Percent numerical frequencies of small mammals in the diets of five predators at Fray Jorge National Park, north-central Chile, throughout 11 biological seasons (wintering and breeding). A + indicates that this species is found in the diet more than expected from its field abundance (Table 1); a − indicates the opposite; a = indicates that this species is taken as expected. P(bi) is the significance level of a binomial test applied to the signs; $P(\chi^2)$ corresponds to a Chi-square test applied to observed (this table) and expected frequencies of small mammals (Table 1). np = no pellets were found, nt = not testable because of lack of degrees of freedom.

Species	W89	B89	W90	B90	W91	B91	W92	B92	W93	B93	W94	No −	No +	P(bi)
Great horned owl														
Abrocoma bennetti	8.7+*	13.8+*	7.7+*	0.7−	0.0−*	1.5+*	1.4+*	0.0−*	0.0−*	0.0−*	0.0−*	6	5	1.000
Abrothrix longipilis	0.4−	0.4−*	0.0−*	0.0=*	0.0=*	1.5−*	0.0−	6.3−*	0.0−*	0.7−	0.0−	9	0	0.004
Akodon olivaceus	4.5−	0.8−	0.0−	2.2−*	0.0−*	20.9−	7.1−	2.1−	2.9−	1.4−	0.9−	11	0	0.002
Octodon degus	38.5−	50.2+	58.0+	46.6+	75.0+	25.4+*	34.3+*	54.2+	46.7+	87.6+	98.3+	1	10	0.012
Oligoryzomys longicaudatus	0.0−*	0.0−	1.2−	4.7+*	0.0=*	4.5−	18.6−	4.2+*	2.9+*	0.0−*	0.0=*	6	3	0.508
Phyllotis darwini	46.4+	30.5+	30.2+	36.9−	25.0−	43.3+	31.4+	33.3+	43.8+	8.3−	0.9−*	4	7	0.548
Thylamys elegans	1.5−*	4.2−	3.0−	9.0+	0.0−*	3.0−*	7.1+*	0.0−*	3.8+*	2.1=*	0.0−*	7	3	0.344
Total (n)	265	239	169	279	56	67	70	48	105	145	117			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			
Barn owl														
Abrocoma bennetti	1.4+*	8.3+*	7.4+*	6.5+*	0.0−*	0.0−*	0.0−*	0.0−*	0.2−	0.5−	3.3+*	6	5	1.000
Abrothrix longipilis	1.4−*	0.0−*	0.0−*	0.0=*	0.0=*	12.5+*	4.3−	4.3−	4.4−	9.6−	4.4−	8	1	0.004
Akodon olivaceus	4.3−	8.3−	0.8−	0.0−*	23.1+*	15.0−	24.9−	21.2−	24.3−	7.1−	8.9−	10	1	0.012
Octodon degus	7.2−	27.4−	10.7−	22.6−	30.8−	7.5+*	1.0−	3.8−	1.7−	24.2−	33.3−	10	1	0.012
Oligoryzomys longicaudatus	1.4+*	0.0−*	5.0−	22.6+*	0.0=*	5.0−*	12.0−	6.3+*	5.7+	4.5+*	6.7+*	4	6	0.754
Phyllotis darwini	81.2+	50.0+	74.4+	22.6−	23.1−*	47.5+	50.7+	56.7+	62.4+	51.0+	43.3+*	2	9	0.066
Thylamys elegans	2.9+*	6.0−	1.7−	25.8+*	23.1+*	12.5+*	7.2+*	7.7+*	1.3+	3.0+*	0.0−*	3	8	0.226
Total (n)	69	84	121	31	13	40	209	208	841	198	90			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	>0.1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			
Burrowing owl														
Abrocoma bennetti	4.7+*	18.8+*	17.6+*	0.0−*	16.7+	14.3+	0.0−*	2.7+*	3.4+*	1.6−*	11.3+*	3	8	0.226
Abrothrix longipilis	14.0+*	0.0−*	11.8+*	0.0=*	0.0=	0.0−	0.0−*	0.0−*	0.9−*	0.8−	0.0−	7	2	0.180
Akodon olivaceus	4.7−	18.8+*	23.5+*	13.8+*	0.0−	28.6−	22.9−	19.1−	13.7−	7.1−	9.4−	8	3	0.226
Octodon degus	9.3−	25.0−	0.0−	37.9−	0.0−	0.0−	2.9−*	0.9−	0.0−	23.8−	18.9−	11	0	0.012
Oligoryzomys longicaudatus	2.3+*	0.0−*	11.8+*	17.2+*	0.0=	0.0−	42.9+	5.5+*	0.9−*	0.0−*	0.0=*	4	5	1.000
Phyllotis darwini	65.1+	37.5+*	29.4=	20.7−	83.3+	57.1+	22.9+	62.7+	81.2+	64.3+	60.4+*	1	9	0.002
Thylamys elegans	0.0−*	0.0−*	5.9−*	10.3+*	0.0−	0.0−	8.6+*	9.1+*	0.0−*	2.4+*	0.0−*	7	4	0.548
Total (n)	43	16	17	29	6	7	35	110	117	126	53			
$P(\chi^2)$	<0.001	>0.1	<0.005	<0.005	nt	nt	<0.005	<0.001	<0.001	<0.001	<0.001			
Pygmy owl														
Abrocoma bennetti	np	np	np	np	0.0−	25.0+	0.0−*	0.0−	0.0−*	0.0−*	np	5	1	0.218
Abrothrix longipilis	np	np	np	np	100+	0.0−	27.3+*	0.0−	11.5+*	13.3+*	np	2	4	0.688
Akodon olivaceus	np	np	np	np	0.0−	25.0−	18.2−	50.0+	26.9−	46.7+	np	4	2	0.688
Octodon degus	np	np	np	np	0.0−	0.0−	0.0−*	0.0−	11.5−	0.0−	np	6	0	0.032
Oligoryzomys longicaudatus	np	np	np	np	0.0=	25.0+	9.1−*	0.0−	3.8+*	0.0−*	np	3	2	1.000
Phyllotis darwini	np	np	np	np	0.0−	25.0+	45.5+*	50.0+	46.2+*	40.0+*	np	1	5	0.218
Thylamys elegans	np	np	np	np	0.0−	0.0−	0.0−*	0.0−	0.0−*	0.0−*	np	6	0	0.032
Total (n)	np	np	np	np	1	4	11	2	26	15	np			
$P(\chi^2)$	nt	nt	nt	nt	nt	nt	>0.05	nt	<0.05	<0.001	nt			
Culpeo fox														
Abrocoma bennetti	55.0+*	56.7+*	45.7+*	31.1+	54.1+*	36.2+*	26.2−*	30.0+*	29.6+*	32.9+*	45.3+*	0	11	0.002
Abrothrix longipilis	0.0−*	0.0−*	0.7−*	0.0=*	0.0=*	2.7−	3.4−	1.6−	0.0−	1.9−	0.0−	9	0	0.004
Akodon olivaceus	0.9−	0.0−	1.3−	2.5−*	0.4−*	10.1−	8.3−	4.5−	4.4−	0.0−	0.0−	11	0	0.002
Octodon degus	26.1−	30.0−	27.8−	54.0+	39.7−	27.5+*	38.6+	45.8+	55.6+	61.5+	54.7−	5	6	1.000
Oligoryzomys longicaudatus	0.0−*	0.0−*	2.6−	0.6+*	0.0=*	4.0−	0.7−	1.6+*	0.0−*	0.0−*	0.0=*	7	2	0.180
Phyllotis darwini	17.1−	13.3−	21.9−	10.2−	5.7−	19.5+	21.4+	16.5−	10.4−	3.7−	0.0−*	9	2	0.066
Thylamys elegans	0.9−*	0.0−	0.0−	1.6−	0.0−	0.0−	1.4−*	0.0−*	0.0−*	0.0−*	0.0−*	11	0	0.002
Total (n)	111	60	151	322	229	149	145	310	135	161	95			
$P(\chi^2)$	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			

* Species pooled for Chi-square calculation.

Table 6. Association between rainfall and productivity features at Fray Jorge National Park, north-central Chile, throughout six years. Note the heavy rains associated with El Niño disturbance of 1991–92. Number and cover of plant species were measured in September each year, whereas seed densities were measured in August ($n = 4$ in all cases; detailed data in Gutiérrez et al. unpubl.). Densities of small mammals and of predators are averages of wintering and breeding seasons reported in Tables 2 and 3, respectively.

Characteristics	1989	1990	1991	1992	1993	1994
Rainfall (mm)	89	32	233	229	77	35
No. perennial plant species	17	15	20	20	20	20
% perennial cover	59	58	62	58	58	54
No. ephemeral plant species	26	26	53	55	46	50
% ephemeral cover	28	11	97	55	13	21
No. perennial seeds/m^2	5817	3607	22967	13914	13844	15771
No. ephemeral seeds/m^2	10927	11333	8840	15824	8292	9954
No. small mammals/ha	15	12	26	117	111	43
No. diurnal predators/750 ha	11	12	7	17	17	14

Functional response of predators

It appears that all four owls cued in on *P. darwini* as a staple prey, but the great horned owl shifted away from it and more toward *O. degus* as the latter species became abundant (Table 7). The Culpeo fox underconsumed *P. darwini*, appeared to key on *A. bennetti* (which no owl did), and shifted toward *O. degus* as it became abundant. This large-sized rodent (second only to *A. bennetti*) was underconsumed by the three smaller owls, likely because it fell out of their killing and handling capabilities (cf. Meserve et al. 1987, Jaksic et al. 1992). The rodents *A. longipilis*, *A. olivaceus*, *O. longicaudatus*, and the marsupial *T. elegans* were generally underconsumed by all five predators. Only the barn owl appeared to select the marsupial.

Two features of predator selectivity require further discussion (Table 7). *Octodon degus* is labelled as a diurnal/crepuscular rodent, thus rendering it puzzling that the evidently nocturnal great horned owl preys on it. However, the only study to date that has quantitatively timed captures of central Chilean small mammals (Iriarte et al. 1989a), reported that *O. degus* has an activity period that extends before dawn, and beyond dusk even to dark night. Therefore, this species is available to strictly nocturnal hunters. The other interesting aspect is that the two largest predators in the area – great horned owl and Culpeo fox – are the only ones that apparently select *O. degus* and *A. bennetti*, the two largest-sized mammal prey at the study site. Either size-selectivity on the part of the large predators, inability of the smaller predators to kill and handle those prey species, or both, may explain the pattern here reported (cf. Iriarte et al. 1989b, Jaksic 1989b, Jaksic et al. 1992).

Guild response of predators

Three possible guild responses to the ENSO disturbance may have been predicted: changes in guild size (number of species per guild), structure (similarity levels at which guilds form), and membership (species composition of each guild).

Throughout the study, two guilds were recognized, a mammalivorous one with generally two species, and an omnivorous one with generally three species. The absence of the pygmy owl during the first four seasons, and during the last season of the study, was the only factor contributing to changes in guild size. We suspect, however, that the absence of this owl was more an artifact of not finding its pellets and feeding roosts than of its not residing at the study site. The statistical distribution of guild nodes did not differ significantly between the first five seasons (Pre-ENSO) and the six latter seasons. Thus, no clear differences were observed in guild size or structure before or after the ENSO disturbance.

Instead, changes in membership were conspicuous in both the mammalivorous and omnivorous guilds. The mammal-eating guild formed by the great horned and barn owl persisted until the breeding season of 1991, and was characterized by a high, shared consumption of *P. darwini* and *A. bennetti*. Thereafter, the great horned owl and Culpeo fox formed a mammalivorous guild that was characterized by the high, shared consumption of *A. bennetti*. Except for two seasons, the barn owl became more closely associated with their omnivorous relatives, burrowing and pygmy owl, due to its continued predation on *P. darwini* and a shift from *A. bennetti* toward *A. olivaceus*.

Predation impact on small mammals

Most predation on local small mammals seemed to be exerted by the four owls and one fox whose diets were studied here. Large hawks are important mammal predators elsewhere (e.g., Jaksic et al. 1992), but were mostly seen traversing but not hunting in the study site. Reptilian predators were scarce: Chilean racerunners, in addition to being mainly insectivorous, have a very limited activity season because of their being heliothermic (Castro et al. 1991). This also applies to long-tailed

Table 7. Summary of apparent prey preferences for predators at Fray Jorge National Park, north-central Chile. Symbols: + = taken more frequently than expected from trapping data; − = taken less frequently; 0 = taken about as expected; +/− and −/+ = apparent preferences shift over time. Activity periods are: D = Diurnal; C = Crepuscular; N = Nocturnal; DCN = Continuously active.

Mammal prey	Weight (g)* $X \pm$ SD	(*n*)	Activity	*B. virginianus* 1227 ± 197 6 (N)	*T. alba* 307 ± 22 (8) CN	*S. cunicularia* 247 ± 22 (3) CN	*G. nanum* 81 ± 13 (3) DCN	*P. culpaeus* 6520 ± 3019 (5) CN
A. bennetti	201.2 ± 46.1	(12)	N	0	0	0	−	+
A. longipilis	54.3 ± 8.8	(38)	N	−	−	−	0	−
A. olivaceus	32.3 ± 5.3	(70)	DCN	−	−	−	0	−
O. degus	140.9 ± 20.9	(46)	DC	+	−	−	−	−/+
O. longicaudatus	24.4 ± 3.0	(14)	N	−	0	0	0	−
P. darwini	58.2 ± 13.7	(124)	N	+/−	+	+	+	−
T. elegans	22.6 ± 9.5	(5)	N	−	+	0	−	−

* Weights for small mammals from Meserve et al. (1987); owl weights from Jaksic et al. (1992); fox weight from Meserve et al. (unpubl.).

snakes, which may need no more than thirty-two 30-g rodents to survive and reproduce successfully over a whole year (Bozinovic and Rosenmann 1988).

Based on their food habits and selectivities, it may be predicted that the experimental exclusion of owls and foxes from the study site should result in population increases of chiefly *O. degus*, *P. darwini*, and *A. bennetti*. Indeed, Meserve et al. (1993b, 1996) demonstrated strong effects of predation on the survivorship and demography of *O. degus* and Lagos et al. (1995) documented marked effects on microhabitat use by this rodent between predator open and predator exclusion grids. Meserve et al. (1996) found that *P. darwini* showed a significant response to the absence of predators, with larger population size and higher survivorship on predator exclusion grids. Unfortunately, *A. bennetti* has been characterized by low levels of trappability at the study site, such that statistically significant effects of predator exclusion have been difficult to detect (Meserve et al. 1996).

On the other hand, we would not expect any major effect of predator exclusions on the remaining mammal species, which were generally taken in proportion or less than expected relative to their field abundances. This was the case for *A. olivaceus* and *O. longicaudatus*, two other species for which Meserve et al. (1996) found no significant predator exclusion responses except for some minor survival differences.

ENSO effects: a bottom-up scenario

Since the influential papers of Paine (1966) and Harper (1969), most students of predation and herbivory have focused on the effects of consumers on their prey diversity, be that of animals, plants or algae (see examples in Fuentes and Jaksic 1988). Demonstrations that some top predators or herbivores act as keystone species, whose removal or addition causes dramatic changes in prey species composition and abundance (cascading effects) have conveyed the general impression that predation effects proceed from top to bottom (e.g., Estes and Palmisano 1974, Castilla and Durán 1985, Kitching 1986, Moreno et al. 1986).

For the terrestrial ecosystem here analyzed, it appears that ENSO effects do not cascade down from higher to lower trophic levels, but the opposite. In this bottom-up scenario, we predict that as primary productivity varies with rainfall, so should secondary (i.e., mammal prey densities), and tertiary productivity (i.e., vertebrate predator densities). Over 5.5 yr we were able to follow both an increase and decrease phase in Fray Jorge, but a new ENSO cycle is needed to determine whether the system behaves as postulated. Long-term monitoring of this terrestrial ecosystem should provide the acid test for this prediction.

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