The components of predation on small mammals in semiarid Chile: preliminary results

Los componentes de la depredación sobre micromamíferos en Chile semiárido: resultados preliminares

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ABSTRACT

We studied a vertebrate predator-mammalian prey system over a two-year period to determine whether predators displayed numerical and (or) functional responses to fluctuations in prey resources. Relative abundances and diets of owls (*Athene cunicularia, Bubo virginianus*, and *Tyto alba*), and of foxes (*Pseudalopex culpaeus*) were determined monthly over a two-year period, simultaneously with assessments of mammalian abundances (six species of Rodentia and one of Marsupialia) at a semiarid site in north-central Chile. Mammal abundances reached maximum levels during the autumn of the two years, and declined during the respective springs, with summer and winters showing intermediate abundances. Except for *P. culpaeus*, the remaining three predators failed to demonstrate numerical responses to the changes in abundance of local small mammals. Except for *B. virginianus*, the remaining three predators did not increase their diet breadths consistently in response to reductions of mammal abundance. All predators showed strong prey preferences for some mammalian species, regardless of their abundance in the field, and thus failed to display functional responses, specifically prey switching. Comparison with similar studies suggest that numerical and functional responses are uncoupled components of predation on small mammals, occurring in all possible combinations. We speculate that only when both responses are displayed simultaneously (a necessary but not sufficient condition), predators may effectively affect mammal abundance.

Key words: Numerical response, functional response, owls, hawks, foxes, rodents, marsupials, South America.

RESUMEN

Estudiamos un sistema predador-presa de vertebrados a lo largo de un período de dos años para determinar si es que los predadores presentaban respuestas numéricas y/o funcionales a las fluctuaciones en los recursos presa. Las abundancias relativas y dietas de las lechuzas (*Athene cunicularia, Bubo virginianus, Tyto alba*) y zorros (*Pseudalopex culpaeus*) se determinaron mensualmente por dos años, simultáneamente con evaluaciones de las abundancias de micromamíferos (seis especies de Rodentia y una de Marsupialia) en una localidad semiárida del centro-norte de Chile. Las abundancias de micromamíferos alcanzaron niveles máximos durante el otoño de ambos años, y declinaron durante las respectivas primaveras. Los veranos e inviernos fueron intermedios al respecto. Excepto por *P. culpaeus*, los restantes tres predadores no demostraron respuestas numéricas a los cambios poblacionales de los micromamíferos. Excepto por *B. virginianus*, los restantes tres predadores no incrementaron consistentemente sus amplitudes de dieta en respuesta a reducciones de la abundancia de micromamíferos. Todos los predadores mostraron fuertes preferencias por algunas especies de micromamíferos, independientemente de sus respectivas abundancias en el terreno, y por ello no mostraron respuestas funcionales, particularmente en alternancia de presas. Comparaciones con estudios similares sugieren que las respuestas numéricas y funcionales son componentes desacoplados en la depredación de vertebrados sobre micromamíferos, dándose en todas las combinaciones posibles. Especulamos que solamente cuando ambas respuestas ocurren simultáneamente (una condición necesaria pero no suficiente), los predadores pueden efectivamente afectar las abundancias de micromamíferos.

Palabras claves: Respuesta numérica, respuesta funcional, lechuzas, halcones, zorros, roedores, marsupiales, Sudamérica.

INTRODUCTION

Predation levels experienced by small mammals depend essentially on two types of attributes: their own vulnerability and their predators' selectivity. Some mammalian species may be rendered more vulnerable to predation than others because of conflicting demands imposed by their morphology, physiology, ecology, behavior, and life history traits

(Taylor 1984). For example, herbivorous rodents may need to feed away from their shelters, thus increasing their risk of predation. At the same time they may reduce that risk by feeding at times when predators are less active or by being socially organized so that some individuals act as sentries while the rest feed. Predators, on the other hand, because of their own phenotypic attributes and constraints, may form more or less specific search images for prey. They may cue in on habitat features where they are more successful while hunting for mammals (e.g., open areas), or they may cue in on specific prey types, e.g. the most abundant or easily caught, the largest or most profitable mammal (Jaksic 1989a, 1989b).

Mammalian prey vulnerability is difficult to assess and even more difficult to interpret. If by some criterion vulnerability were found to be especially high for a given mammal species, it is always possible to provide ad-hoc "explanations" ranging from historical inertia to contemporary compromises of opposing selective forces. By comparison, predator selectivity may be more objectively measured, because all that is required in principle is a tally of the prey consumed as gauged by the abundance of that prey in the habitat patches where and when the predator hunts. However, this assessment requires thorough knowledge of habitat and time use by both predators and potential prey (Hansson 1989). The task of attaining such measurements becomes more and more complex as the number of predator and prey species increases.

Perhaps for this latter reason, studies of predator-mammalian prey interactions have tended to focus on either one or a few predator species hunting for several mammalian prey (Phelan & Robertson 1978, Nilsson 1981, 1984, Marks & Marti 1984, Korpimäki 1985a, 1987, Steenhof & Kochert 1985, 1988, Corbett & Newsome 1987, Korpimäki & Norrdahl 1991), or on a single mammalian species being hunted by one or several predator species (Boonstra 1977, Beacham 1979, Taitt & Krebs 1983, Janes & Barss 1985, Lindström *et al.* 1986, Pearson 1985, Desy & Batzli 1989, Trout & Tittensor 1989, Sinclair *et al.* 1990, Steen *et al.* 1990).

Few studies have attempted to evaluate predator-mammalian prey interactions on a collective basis, and these have been conducted mainly in Scandinavia (Andersson & Erlinge 1977, Hörnfeldt 1978, Erlinge *et al.* 1982, 1983, 1984, Angelstam *et al.* 1984, Korpimäki 1984, 1985b, 1986, Erlinge 1987, Hansson 1987, Korpimäki & Norrdahl 1989, 1991). Notable exceptions in North America are the field studies of Kotler (1984, 1985), Brown *et al.* (1988), Kotler *et al.* (1988), Brown (1989), and Kotler & Holt (1989), although these have emphasized only the effects of owl predation on community structure and ecomorphology of rodents.

The paucity of equivalent information from the Neotropical region is striking. Most of the research on predator-mammalian prey interactions seems to have been restricted to Chile and Argentina (reviews in Jaksic 1986, Jaksic & Simonetti 1987, Simonetti 1989), with the same biases noted above, and with the additional shortcoming of having been short-term. Here we report a study carried over two years in a semi-arid scrub community of north-central Chile, where the phylogenetically diverse mammalian prey and the syntopic predator assemblage were studied simultaneously.

The theoretical framework of our study refers to the two major components of vertebrate predation: the numerical and functional responses showed by predators when facing fluctuating mammalian prey populations. When prey abundance increases, predators may respond numerically by dispersing from peripheral areas and (or) reproducing successfully (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 & Oaten 1975), whereby they change their selection of prey depending on the relative frequency that prey are encountered in the field. We test whether numerical, functional, or both responses are displayed by predators faced with fluctuating prey resources at our study site, and compare our results with those from other studies. Our results and conclusions are preliminary because this is a foregoing research. The study period covered

in this report was unusually dry, and as the system returns to its normal precipitation regime, both prey and predators may change their dynamics of interaction.

STUDY AREA AND METHODS

Study area

The study area is located in a semi-arid mediterranean scrub community in Quebrada de las Vacas (200 m elevation), an interior valley in Fray Jorge National Park (30° 38' S, 71° 40' W, IV Administrative Region of Chile). This low elevation scrub zone contains spiny drought-deciduous and evergreen shrubs, and an herbaceous understory, on a predominantly sandy substratum. The most characteristic plant associations are those of *Porlieria chilensis - Proustia pungens - Adesmia bedwellii* (Muñóz & Pisano 1947), and mean shrub cover averages 59% (Meserve 1981a, 1981b). The semi-arid mediterranean climate of this area has 90% of the mean 85 mm annual precipitation falling between May - September (from late autumn to early spring in the Southern Hemisphere), and warm, dry summers.

Small mammal 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 throughout 4 days/month with two Sherman-type live traps/station. Standard mark and release techniques (Meserve & Le Boulengé 1987) are used with data taken on small mammal species, number, trap station, sex, reproductive condition, and weight.

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 & Le Boulengé 1987). Trappability was generally high (>70%) for most species, enabling use of enumeration techniques. Monthly MNKA estimates on the four control grids were averaged together and then pooled for the three month periods corresponding to major austral seasons: summer (December-February), autumn (March-May), winter (June-August), and spring (September-November), for generation of "expected" frequencies of small mammals in predator diets (e.g. Pearre 1982).

Predator abundance and residence status

Records were kept on the presence of vertebrate predators at the study site starting October 1988 (austral spring). Predators were categorized as either residents (when their presence was recorded daily on average) or occasional (when their presence was more sporadic).

A quantitative estimate of the relative abundance of diurnal raptors was obtained by recording the number of sightings of different raptor species per day of field work during monthly visits to the study site. The observation effort was standardized to 9 h daily, to render the data comparable. Approximately 750 ha in the vicinity of the trapping grids in Quebrada de las Vacas were covered by this visual tally.

Starting in December (summer) 1988, an indirect estimate of the relative abundance of owls was obtained by collecting regurgitated pellets under the same roosting and nesting sites during every monthly session in the field, as standardized by the number of days spent in every session. We assume that we found all major roosting and nesting sites within the study site. The relative abundance of foxes was assessed by collecting feces within the immediate vicinity of the trapping grids (see below). Use of these data to indirectly assess relative changes in predator numbers follows the methodology of Sinclair *et al.* (1990).

Predator food habits

Fresh pellets and feces were collected on a monthly basis from December (summer) 1988 through February (summer) 1991. Regurgitat-

ed pellets of both diurnal and nocturnal raptors were collected under known roosts, nests, or perches. 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 voucher specimens locally collected. 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 we did not overlook the presence of any of those species in their diets.

Throughout the study period we monitored the relative representation of major prey groups in the diets of those predators that were site residents. We estimated diet breadth as $B = 1/\Sigma (p_i^2)$, where p_i is the relative occurrence of prey category i in a given predator's diet. This index yields values ranging between 1 and n (for n equally used categories; see Levins 1968) and reflects population-wide use of resources regardless of their relative availability (Feinsinger *et al.* 1981). We computed diet breadth across broad prey categories only (i.e. mammals, birds, reptiles, amphibians, insects, and arachnids), each of which likely requires different detection abilities, foraging techniques, and capture methods on the part of the predators.

Predator selectivity

Chi-square goodness-of-fit tests were made between observed frequencies of small mammals in predator diets, and the expected frequencies generated from trapping data (Pearre 1982). Small mammal species were pooled whenever necessary to obtain expected frequencies > 5, as required by the Chi-square test (Sokal & 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.

Nomenclature

For mammals, scientific names follow Honacki *et al.* (1982; except for foxes, where we follow Berta 1987) and vernacular names follow Tamayo *et al.* (1987). For birds, both scientific and vernacular names follow Araya (1985). For reptiles and amphibians, scientific names follow Donoso-Barros (1966) and Díaz (1983), respectively; vernacular names are ad-hoc. For scientific names of plants, we follow Muñóz & Pisano (1947), and Hoffmann (1980).

RESULTS

Small mammal abundance

Total abundance of small mammals reached a maximum during the autumn of 1989 and declined through winter and spring to recover during the summer of 1990. The same pattern was observed between autumn 1990 and summer 1991 (Table 1). Spring density during 1989 was only 20% that of the preceding autumn, and during 1990 it was 36% of that observed in autumn (Table 1). Maximum abundances during the autumn result from the cumulative reproductive effort of local small mammals, which start reproducing during early spring (Fulk 1976, Meserve & Le Boulengé 1987).

Seven species of small mammals were captured throughout the study period. The Fence degu-rat (*Octodon degus*), Darwin's leaf-eared mouse (*Phyllotis darwini*), and Olivaceous field-mouse (*Akodon olivaceus*) were the most abundant species at the site. They accounted for an overall 41%, 28%, and 13% of small mammal captures, respectively (Table 1). These three species were captured during all seasons, and their coefficients of variation for population abundance were the lowest. The remaining four species together accounted for only 8% of total captures. Of these, Bennett's chinchilla-rat (*Abrocoma bennetti*), Long-haired field-mouse (*Akodon longipilis*), and Long-tailed rice-rat (*Oryzomys longicaudatus*) were not captured at all during entire seasons, thus demonstrating relatively high coefficients of variation (Table 1). The Llaca mouse-opossum (*Marmosa elegans*), although not abundant, was present throughout

TABLE 1

Small mammals trapped at the study site. Numbers are estimated absolute
(number/ha) and relative densities by season, extrapolated from estimates
of minimum number known to be alive on four trapping grids

Micromamíferos capturados en el sitio de estudio. Los números son las densidades estacionales absolutas (número/há)
y relativas, extrapoladas de estimaciones del número mínimo conocido vivo en cuatro grillas de trampeo

Small mammals	Autumn 89		Winter 89		Spring 89		Summer 90		Autumn 90		Winter 90		Spring 90		Summer 91		Overall	
	No/ha	%	No/ha	%	No/ha	%	No/ha	%	No/ha	%	No/ha	%	No/ha	%	No/ha	%	Mean	%CV
Abrocoma bennetti	0.5	0.7	0.8	1.8	0.0	0.0	0.0	0.0	1.0	1.7	0.3	0.7	1.0	4.7	1.3	5.0	0.6	81.0
Akodon longipilis	4.3	5.8	5.5	13.0	2.0	13.8	1.3	2.4	2.0	3.3	0.5	1.4	0.0	0.0	0.0	0.0	1.9	103.4
Akodon olivaceus	10.0	13.7	6.5	15.4	4.3	29.3	5.0	9.8	5.3	8.8	6.0	16.3	1.3	5.9	1.0	4.0	4.9	59.1
Marmosa elegans	1.8	2.4	0.8	1.8	1.5	10.3	6.5	12.7	5.8	9.6	1.8	4.8	2.0	9.4	1.5	6.0	2.7	80.4
Octodon degus	40.3	54.9	22.0	52.1	4.0	27.6	20.5	40.0	20.8	34.6	14.8	40.1	8.8	41.2	9.3	37.0	17.5	64.4
Oryzomys longicaudatus	0.0	0.0	0.3	0.6	0.3	1.7	3.0	5.9	4.8	7.9	5.5	15.0	0.0	0.0	0.0	0.0	1.7	136.1
Phyllotis darwini	16.5	22.5	6.5	15.3	2.5	17.3	15.0	29.2	20.5	34.1	8.0	21.7	8.3	38.8	12.0	48.0	11.2	53.2
Total	73.4	100.0	42.4	100.0	14.6	100.0	51.3	100.0	60.2	100.0	36.9	100.0	21.4	100.0	25.1	100.0	40.5	50.0

the study period, and showed an intermediate coefficient of variation (Table 1).

Predator abundance and residence status

Two diurnal raptors were residents at the study site: the Black-chested Eagle (*Geranoaetus melanoleucus*) and the Chimango Caracara (*Milvago chimango*). These two raptors were observed flying over (infrequently perching) during all seasons, with only small numerical fluctuations, as demonstrated by their low coefficients of variation (Table 2). 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 demonstrated markedly higher coefficients of variation, being absent from the study site during whole seasons (Table 2). The remaining four diurnal raptors, Cinereous Harrier (*Circus cinereus*), Black-shouldered Kite (*Elanus caeruleus*), Peregrine Falcon (*Falco peregrinus*), and Aplomado Falcon (*Falco femoralis*), were of sporadic occurrence at the study site, sighted only during one or two field seasons (Table 2).

Three species of owls were residents at the study site, and their pellets were collected daily on average through all seasons in the field (Table 2). They were the Burrowing Owl (*Athene cunicularia*), Great Horned Owl (*Bubo virginianus*), and Common Barn Owl (*Tyto alba*). A fourth species, the Austral Pygmy Owl (*Glaucidium nanum*) may also be resident at the study site. We identified its vocalizations, but could not find pellets or its conspicuous feather-plucking perches (Jiménez & Jaksic 1989a). Despite Fulk's (1976) report, we did not observe Short-eared Owls (*Asio flammeus*) at the study site.

Only one species of mammalian carnivore was a year-round resident at the study site, the Colpeo fox (*Pseudalopex culpaeus*). The Pampas cat (*Felis colocola*), Lesser grison (*Galictis cuja*), and Hog-nosed skunk (*Conepatus chinga*) have all been reported from the park, but we did not observe them, except for tracks of an unidentified mustelid, and the occasional musk odor of skunk.

Reptilian predators were sporadically seen and consisted of only the Long-tailed snake (*Philodryas chamissonis*) and the Chilean racerunner (*Callopistes palluma*), both diurnally active.

TABLE 2

Relative abundances of predators at the study site, by season. Figures are number
of sightings (diurnal raptors) or of pellets (nocturnal raptors) and feces (mammalian carnivores),
obtained in any given season, standardized by the number of days spent in the field

Abundancias relativas de predadores en el sitio de estudio por estación. Las cifra son el número
de avistamientos (rapaces diurnas) o de egagrópilas (rapaces nocturnas) y de fecas (mamíferos carnívoros)
obtenidos en una estación dada, estandarizados por el número de días pasados en terreno

Seasons	Spring 88	Summer 89	Autumn 89	Winter 89	Spring 89	Summer 90	Autumn 90	Winter 90	Spring 90	Summer 91	Mean	CV (%)
Days sampled	19	27	29	28	23	25	23	26	27	27	n = 10	n = 10
Geranoaetus melanoleucus	0.63	1.11	1.28	0.71	1.48	1.48	2.13	2.35	1.30	0.67	1.31	44.7
Milvago chimango	0.11	0.04	0.97	2.00	1.52	1.32	1.52	2.04	0.74	0.15	1.04	73.1
Parabuteo unicinctus	1.11	2.04	0.21	0.00	0.04	0.24	0.26	0.04	0.11	0.00	0.40	163.4
Buteo polyosoma	0.47	0.15	0.21	0.14	0.26	0.12	0.04	0.00	0.11	0.00	0.15	93.6
Falco sparverius	0.00	0.00	0.00	0.25	0.00	0.28	0.17	0.54	0.15	0.15	0.15	112.3
Circus cinereus	0.11	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	242.4
Elanus caeruleus	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.00	0.01	315.6
Falco peregrinus	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.00	0.01	316.4
Falco femoralis	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.01	316.3
Total raptor sightings/day	2.58	3.33	2.69	3.11	3.30	3.44	4.22	4.96	2.41	0.96	3.10	35.4
Days sampled	19	27	29	28	23	25	23	26	27	27	n = 9	n = 9
Athene cunicularia	nd*	0.67	2.93	2.32	4.13	3.16	5.09	3.46	3.59	2.85	3.13	38.7
Bubo virginianus	nd	2.00	3.41	4.36	4.35	4.88	3.13	3.73	4.89	3.22	3.77	24.8
Tyto alba	nd	1.26	1.34	1.29	1.96	1.72	1.52	3.15	0.78	0.26	1.48	54.6
Pseudalopex culpaeus	nd	2.33	4.28	3.04	2.00	3.96	5.00	4.62	4.19	6.67	4.01	36.2
Total pellets & feces/day	nd	6.26	11.97	11.00	12.43	13.72	14.74	14.96	13.44	13.00	12.39	20.8

*nd = No data; pellets and feces were not collected because they were of unknown age.

Predator food habits

Overall, 1950 pellets and 945 feces were collected, and 7886 prey items were identified. The presence of plant material (mostly fruit seeds) in fox feces was also recorded. Pellets of the five resident raptors were collected, but only those of Burrowing Owls, Great Horned Owls, and Common Barn Owls, were found in all months. Pellets of Black-chested Eagles and Chimango Caracaras were infrequent. 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 fewer pellets. Foxes provided consistent monthly numbers of feces. No effort was made to collect feces of either Long-tailed snakes or Chilean racerunners.

Burrowing Owls ate primarily insects and arachnids (combined figures ranged 69-96% throughout the study period), but also some mammals (1-31%). A steady decline in consumption of mammalian prey was observed throughout 1989, with a subsequent stabilization at 1-6% (Table 3). Darwin's leaf-eared mouse was its most common prey. Birds and reptiles were rarely found as prey, but amphibians were more prevalent, reaching a high of 13% (Table 3). These amphibians were all terrestrial toads (*Bufo chilensis*), and were only partly consumed, as the owls discarded the intestines and the apparently distasteful integument. Diet breadth was not associated to trends in mammal abundances. Although mammals reached maximum levels during autumn 1989 and declined during spring 1989, diet breadths of Burrowing Owls did not change. During 1990, when minimum mammal densities were not as low as the preceding year, diet breadth of the owls increased by 77% (Table 3).

Great Horned Owls ate primarily mammals (70-98% of its prey throughout the study), without seasonal trends (Table 3). Their most common mammalian prey were, in decreasing order, Darwin's leaf-eared mouse, Bennett's chinchilla-rat, and Fence degu-rat. Birds were consistently taken at low figures (<4% throughout the study period), whereas reptiles and amphibians were only rarely taken (Table

TABLE 3

Diets of predators at the study site. Numbers are percent numerical frequencies among prey, except for fruits, which are percent numerical frequencies among feces. Diet breadth was computed using prey classes as entries

Dietas de los predadores en el sitio de estudio. Las cifras son frecuencias numéricas de presas en la dieta, excepto para frutos, que son frecuencias numéricas en el total de fecas analizadas

	Summer 89	Autumn 89	Winter 89	Spring 89	Summer 90	Autumn 90	Winter 90	Spring 90	Summer 91
A. cunicularia									
Mammals	31.4	10.0	7.0	1.4	5.6	1.1	6.2	4.0	3.6
Birds	0.0	0.2	0.0	0.2	0.0	0.4	0.3	2.5	0.4
Other vertebrates	0.0	0.0	0.9	5.6	1.5	3.7	12.5	0.0	0.1
Invertebrates	68.6	89.8	92.1	92.8	92.9	94.8	81.0	93.5	95.9
No. Prey	70	408	431	504	340	566	321	896	716
Diet Breadth	2.1	1.4	1.3	1.4	1.7	1.3	1.8	2.3	1.9
B. virginianus									
Mammals	95.5	98.4	90.7	69.8	74.6	77.0	96.1	72.5	79.0
Birds	0.0	0.0	2.7	3.1	0.5	1.0	3.9	1.7	0.8
Other vertebrates	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.3	0.0
Invertebrates	4.5	1.6	6.6	27.1	24.9	21.0	0.0	24.5	20.2
No. Prey	89	129	182	159	193	100	102	240	124
Diet Breadth	1.1	1.0	1.2	1.8	1.7	1.6	1.1	1.8	1.5
T. alba									
Mammals	92.3	80.4	83.3	57.5	54.3	70.6	96.8	100.0	80.0
Birds	0.0	2.2	4.2	2.5	2.5	2.0	1.1	0.0	10.0
Other vertebrates	0.0	0.0	8.4	1.3	1.2	0.0	0.0	0.0	0.0
Invertebrates	7.7	17.4	4.1	38.7	42.0	27.4	2.1	0.0	10.0
No. Prey	52	46	48	80	81	51	94	27	10
Diet Breadth	1.2	1.5	1.4	2.4	2.6	1.8	1.1	1.0	1.5
P. culpaeus									
Mammals	78.2	80.8	88.1	6.4	21.8	56.4	56.4	41.4	68.2
Birds	7.7	2.9	7.5	2.1	5.0	3.6	7.9	6.9	5.8
Other vertebrates	3.8	3.8	1.5	2.7	9.6	4.8	2.9	5.2	4.5
Invertebrates	10.3	12.5	2.9	88.8	63.6	35.2	32.8	46.5	21.5
No. Prey	78	104	67	375	239	165	140	348	311
Diet Breadth	1.6	1.5	1.3	1.3	2.3	2.3	2.4	3.1	2.0
% Fruit/Feces	16.3	44.8	33.9	15.2	37.7	13.4	20.3	34.6	24.4

3). Insects and arachnids occurred at widely fluctuating levels in the diet (combined figures ranged 0-27%), without seasonal patterns. A consistent pattern of increased diet breadth during spring versus autumn (Table 3) suggests that as mammal abundances declined, Great Horned Owls increased their consumption of other prey, particularly insects and arachnids. However, much of the invertebrate consumption may be due to juvenile owls (Jaksic, pers. obs.), which are known to be indiscriminate predators as they develop their hunting skills.

Common Barn Owls preyed mainly on small mammals (54-100% of prey occurrences throughout the study period), without seasonal trends (Table 3). With Great Horned Owls they shared the same staple prey, Darwin's leaf-eared mouse and Bennett's chinchilla-rat. However, the Llaca mouse-opossum and the Long-tailed rice-rat were more frequent items than the Fence degu-rat at the end of the study. Birds were consistently taken at low numbers (≤ 10% throughout the study period), but not so reptiles or amphibians (Table 3). Insects and arachnids fluctuated widely (combined figures 0-42%), in phase with the same trends observed among Great Horned Owls, except for spring 1990, when Common Barn Owls preyed exclusively on small mammals. Diet breadths were not clearly related to mammal abundances (Table 3). The owls did increase their diet breadth as small mammals declined in spring 1989, but they failed to do so during spring 1990 (when they actually showed the opposite trend).

Colpeo foxes ate primarily mammals, but with large fluctuations (6-88% of prey occurrences throughout the study period; Table 3). Darwin's leaf-eared mouse and Bennett's chinchilla-rat were frequently eaten by foxes, but their combined representation was often similar to that made up by the Fence degu-rat alone. Birds and reptiles were consistently preyed upon, but their combined occurrence never exceeded 15%. Insects and arachnids together comprised from 3 to 89% of prey occurrences, in keeping with reverse trends of mammal consumption. Fruit seeds were frequent in the feces, without seasonal differences. As mammals declined from autumn to spring, fruit consumption by foxes decreased between these two respective seasons in 1989, and increased between the same seasons

in 1990 (Table 3). Diet breadths showed the same lack of patterns as fruit consumption (Table 3).

We did not obtain sufficient dietary information on the remaining four resident predators, but based on scant qualitative data, their food habits appeared similar to those reported from localities 400 km south of our study site (see below). The Black-chested Eagle apparently uses small mammals as its staple prey. Schlatter et al. (1980) reported that in La Dehesa mammals accounted for 78% of its diet numerically, with the Fence degu-rat being the most common prey. Jiménez & Jaksic (1989b) reported that in San Carlos mammals accounted for 64-75% of its diet, with the Fence degu-rat being the main prey. Chimango Caracaras from Pudahuel prey mostly on insects (87% of its diet by number) and rarely (2%) on mammals (Yáñez et al. 1982). Long-tailed snakes have been reported (Jaksic & Delibes 1987) to prey mainly on reptiles and amphibians (80% by number), and less on mammals (12%). Chilean racerunners are essentially insectivorous (84% of its diet by numbers), with mammals comprising only 9% of prey occurrences (Castro et al. 1991). However, they may prey extensively on small rodents (Mellado 1982).

Predator selectivity

Overall, it appeared that Burrowing Owls (Table 4) selected Bennett's chinchilla-rat (throughout the study), Darwin's leaf-eared mouse (except during spring 1990), and Olivaceous field-mouse (except during autumn-winter 1989). On the other hand, they underconsumed (i. e. took in lower proportion than expected) Fence degu-rat (throughout the study) and Llaca mouse-opossum (except during autumn 1990 and summer 1991). Burrowing Owl predation on Long-haired field-mouse and Long-tailed rice-rat fluctuated erratically.

Great Horned Owls (Table 5) selected Bennett's chinchilla-rat (throughout the study) and Darwin's leaf-eared mouse (except during summer 1990 and 1991), whereas they underconsumed Long-haired field-mouse, Olivaceous field-mouse, and Fence degu-rat throughout the study. They underconsumed Long-tailed rice-rat, except during spring 1990,

TABLE 4

Observed frequencies of small mammals in the diet of Burrowing Owls at the study site,
by season, as determined by pooled minimum numbers of individuals in pellets, compared with
expected frequencies (from Table 1), based on trapping results. Abbreviations are: Observed (Obs),
Expected (Exp), $P(X^2)$ is the significance level of the Chi-square statistic applied to observed
and expected values, n.a. = Not applicable for lack of degrees of freedom

Frecuencias observadas de micromamíferos en la dieta del pequén en el sitio de estudio, por estación, comparada con las
frecuencias esperadas según los respectivos trampeos (calculadas de la Tabla 1). Obs = Observado, Exp = Esperado, $P(X^2)$ =
nivel de significancia de la prueba Chi-cuadrado aplicada a dichos valores, n.a. = no aplicable por falta de grados de libertad

Small mammals	Autumn 89		Winter 89		Spring 89		Summer 90		Autumn 90		Winter 90		Spring 90		Summer 91	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Abrocoma bennetti	3	0.2	1	0.3	0	0.0	4	0.0	0	0.0	0	0.1	10	0.9	1	0.5
Akodon longipilis	0	1.4	6	2.5	0	0.3	0	0.3	0	0.0	2	0.2	0	0.0	0	0.0
Akodon olivaceus	1	3.2	1	3.0	1	0.6	2	1.4	0	0.1	4	2.6	3	1.1	1	0.4
Marmosa elegans	0	0.6	0	0.3	0	0.2	0	1.8	1	0.1	0	0.8	1	1.8	2	0.6
Octodon degus	2	13.2	0	9.9	0	0.6	3	5.6	0	0.3	3	6.4	0	7.8	0	3.7
Oryzomys longicaudatus	0	0.0	1	0.1	0	0.0	0	0.8	0	0.2	2	2.4	4	0.0	1	0.0
Phyllotis darwini	18	5.4	10	2.9	1	0.3	5	4.1	0	0.3	5	3.5	1	7.4	5	4.8
Total	24	24.0	19	19.0	2	2.0	14	14.0	1	1.0	16	16.0	19	19.0	10	10.0
$P(X^2)$	< 0.001		<0.001		n.a.		> 0.15		n.a.		> 0.08		< 0.001		> 0.89	

TABLE 5

Observed and expected frequencies of small mammals in the diet of Great
Horned Owls at the study site, by season (see Table 4 for explanations)

Frecuencias observadas y esperadas de micromamíferos en la dieta del tucúquere en el sitio
de estudio, por estación (véase Tabla 4 para explicaciones)

Small mammals	Autumn 89		Winter 89		Spring 89		Summer 90		Autumn 90		Winter 90		Spring 90		Summer 91	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Abrocoma bennetti	30	0.8	72	2.7	51	0.0	69	0.0	37	1.2	61	0.7	61	7.0	43	3.8
Akodon longipilis	1	6.6	0	19.7	0	14.3	1	3.3	0	2.4	0	1.3	0	0.0	0	0.0
Akodon olivaceus	6	15.6	6	23.2	2	30.5	0	13.2	0	6.4	0	15.7	2	8.6	1	3.0
Marmosa elegans	2	2.7	2	2.7	4	10.8	6	17.1	0	7.0	5	4.5	11	13.8	6	4.6
Octodon degus	3	62.6	20	78.6	9	28.7	24	54.0	5	25.2	8	38.5	2	60.5	2	28.1
Oryzomys longicaudatus	0	0.0	0	0.9	0	1.8	0	7.9	2	5.9	0	14.4	11	0.0	0	0.0
Phyllotis darwini	72	25.7	51	23.2	38	17.9	35	39.5	29	24.9	22	20.9	60	57.1	24	36.5
Total	114	114.0	151	151.0	104	104.0	135	135.0	73	73.0	96	96.0	47	147.0	76	76.0
$P(X^2)$	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

when they ate surprising numbers of this rodent when none was expected. Great Horned Owls also generally underconsumed Llaca mouse-opossum, except during winter 1990 and summer 1991.

Common Barn Owls behaved similarly as Great Horned Owls with respect to prey selection (Table 6). They selected Bennett's chinchilla-rat (throughout the study) and Darwin's leaf-eared mouse (except during spring 1990 and summer 1991), and underconsumed Long-haired field-mouse, Olivaceous field-mouse,

and Fence degu-rat. They underconsumed Long-tailed rice-rat, except during winter 1989, spring 1990, and summer 1991. During the latter two seasons, Common Barn Owls ate some individuals of this rodent when none was expected. Consumption of Llaca mouse-opossum appears to have been erratic.

Colpeo foxes (Table 7) selected Bennett's chinchilla-rat (throughout the study) and Fence degu-rat (except during autumn 1989 and spring 1990), whereas they underconsumed Long-haired field-mouse, Olivaceous field-

TABLE 6

Observed and expected frequencies of small mammals in the diet of
Common Barn Owls at the study site, by season (see Table 4 for explanations)

Frecuencias observadas y esperadas de micromamíferos en la dieta de la lechuza en el sitio
de estudio, por estación (véase Tabla 4 para explicaciones)

Small mammals	Autumn 89		Winter 89		Spring 89		Summer 90		Autumn 90		Winter 90		Spring 90		Summer 91	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Abrocoma bennetti	3	0.3	2	0.7	7	0.0	16	0.0	5	0.5	8	0.6	6	1.1	1	0.4
Akodon longipilis	1	1.9	0	4.7	0	5.5	0	1.1	0	1.0	0	1.2	0	0.0	0	0.0
Akodon olivaceus	1	4.5	2	5.5	5	11.7	2	4.2	0	2.7	1	14.7	0	1.4	0	0.3
Marmosa elegans	1	0.8	1	0.7	4	4.1	1	5.6	0	3.0	2	4.3	6	2.3	2	0.4
Octodon degus	1	18.1	0	18.7	2	11.0	5	17.6	0	10.7	9	36.1	1	9.9	1	2.6
Oryzomys longicaudatus	0	0.0	1	0.2	0	0.8	0	2.6	2	2.5	4	13.5	5	0.0	2	0.0
Phyllotis darwini	26	7.4	30	5.5	22	6.9	20	12.9	24	10.6	66	19.6	6	9.3	1	3.3
Total	33	33.0	36	36.0	40	40.0	44	44.0	31	31.0	90	90.0	24	24.0	7	7.0
P(X²)	< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		n.a.	

TABLE 7

Observed and expected frequencies of small mammals in the diet of Colpeo
foxes at the study site, by season (see Table 4 for explanations)

Frecuencias observadas y esperadas de micromamíferos en la dieta del culpeo en el
sitio de estudio, por estación (véase Tabla 4 para explicaciones)

Small mammals	Autumn 89		Winter 89		Spring 89		Summer 90		Autumn 90		Winter 90		Spring 90		Summer 91	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Abrocoma bennetti	15	0.4	14	0.9	3	0.0	15	0.0	24	1.3	18	0.5	78	6.2	96	9.6
Akodon longipilis	0	3.7	0	6.1	0	2.8	0	1.0	1	2.6	0	1.0	0	0.0	0	0.0
Akodon olivaceus	1	8.6	0	7.4	0	5.9	0	3.9	2	6.8	0	11.9	7	7.7	1	7.7
Marmosa elegans	1	1.5	0	0.9	0	2.1	0	5.1	0	7.5	0	3.5	4	12.3	1	11.5
Octodon degus	32	34.6	29	25.0	14	5.5	20	16.0	31	27.0	38	29.3	24	53.9	77	71.0
Oryzomys longicaudatus	0	0.0	0	0.3	0	0.3	0	2.3	4	6.1	0	10.9	1	0.0	1	0.0
Phyllotis darwini	14	14.2	5	7.4	3	3.4	5	11.7	16	26.7	17	15.9	17	50.9	16	92.2
Total	63	63.0	48	48.0	20	20.0	40	40.0	78	78.0	73	73.0	131	131.0	192	192.0
P(X²)	< 0.001		< 0.005		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001		< 0.001	

mouse, and Llaca mouse-opossum throughout the study. Colpeo foxes also underconsumed Darwin's leaf-eared mouse (except during winter 1990) and Long-tailed rice-rat (except during spring 1990 and summer 1991).

DISCUSSION

Predictable changes in mammalian prey abundance

Local small mammals predictably increased from summer to autumn and declined from winter to spring (Table 1; Meserve & Le Boulengé 1987). The three main components of the local mammalian assemblage (Fence degu-rat, Darwin's leaf-eared mouse, and Olivaceous field-mouse) showed the same temporal pattern of yearly abundances, and consequently their relative abundances did not change as markedly as did their absolute abundances. This feature of mammalian prey may have important implications for predators, because as the most abundant mammals in the area decline seasonally, they may be encountered by predators at a slower rate, but still roughly in the same proportion. This constancy in relative abundance of mammalian prey does not provide a crucial cue for changing the predators' search image, and thus does not facilitate prey switching (Murdoch 1969, Murdoch & Oaten 1975).

Lack of numerical response by predators

Six predator species were year-round residents at our study site (two hawks, three owls, and a fox). Jaksic *et al.* (1992) found that in Aucó, a drier and less vegetated locality some 150 km to the south, numbers of resident predator species fluctuated greatly over time. Up to 10 raptorial and carnivore species concentrated in Aucó during 1987 (when a small-mammal irruption was underway), but all falconiforms vacated the area after the small mammals crashed the following year. During 1988 only six predator species were resident in Aucó, including Burrowing, Great Horned, Austral Pygmy, and Common Barn Owls, together with Colpeo and Grey foxes (*Pseudalopex griseus*). During 1989 and 1990 Common Barn Owls ceased to reside continuously at Aucó, and thus, five resident predators were left. Thus, the composition of the assemblage in Fray Jorge is less variable in time than that in Aucó. Major differences in predator composition between the two sites are that in Fray Jorge there is only one fox species (the Colpeo fox) and that Common Barn Owls, Black-chested Eagles, and Chimango Caracaras are year-round residents there.

Overall sightings of diurnal raptors in our study area did not increase during the first season of high mammalian prey abundance (autumn of 1989), but they did so during the second year (autumn 1990), although the maximum was actually observed the following winter, when mammalian abundance was already declining (Table 2). The same lack of clear-cut pattern was demonstrated by the two resident diurnal raptors (Black-chested Eagles and Chimango Caracaras). It appears then, that diurnal raptors did not respond numerically to the seasonal trend of abundances of mammalian prey.

Overall collections of pellets (owls) and feces (foxes) were remarkably constant throughout the study (Table 2). None of the three owl species consistently increased or decreased their feeding activities in the study site (as judged by pellet counts) in numerical response to the corresponding phases of mammalian prey abundance. Burrowing Owls increased only during the second high season for mammals (autumn 1990), Great Horned Owls did not show any obvious trend, and

Common Barn Owls increased during winter 1990, when mammal prey abundances were the lowest. Foxes, on the other hand, followed the pattern of high and low prey seasons (autumn and spring, respectively) very closely, even to the point of producing intermediate amounts of feces at the seasons of intermediate mammal abundance (winter and summer).

The failure of all raptors (both diurnal and nocturnal) to respond numerically to the mammalian abundances at the study site may simply reflect the fact that they hunt over substantially more extensive areas than those of our trapping grids. Because of their high mobility, they may search and detect patches where mammal prey are more abundant, thus dampening their expected numerical responses. The close fit between fox and mammal abundance may be a consequence of having collected feces in the immediate vicinity of the trapping grids, and not over a broader area. Because foxes also have extensive home ranges at the study site (Meserve *et al.* unpubl. data), and thus, a similar potential as raptors for dampening their expected numerical responses by hunting in patches with higher than average mammal abundance, the observed close fit is puzzling. Perhaps foxes cued their home range to the changing prey abundances by hunting over a more extended area when mammals declined, thus scattering their feces over a broader area. This is not the case of raptors (particularly owls), which despite changing the extension of their hunting ranges, return to the same perching, roosting, or nesting sites, and cast their pellets there.

The overall lack of numerical responses by local predators may be explained by the relatively modest differences between high and low seasons of mammalian abundance. The most dramatic difference occurred the first year of the study, when spring density amounted to only 20% the maximum density observed in autumn. During the concurrent study of Jaksic *et al.* (1992), where some predators did respond numerically by abandoning Aucó, mammal abundances crashed to only 7% of peak densities (Jiménez *et al.* 1992). If mammal abundances would reach this low figure in Fray Jorge, perhaps numerical responses would then be observed.

Insectivorous, carnivorous, and omnivorous predators

The four predators studied may be categorized in the following manner: Burrowing Owls were essentially insectivorous, taking Darwin's leaf-eared mouse particularly among the few small mammals eaten. Great Horned and Barn Owls were carnivorous predators, their staple prey being Darwin's leaf-eared mouse and Bennett's chinchilla-rat. Colpeo foxes were omnivorous, feeding on vertebrates, invertebrates, and fruits. Among mammals, their primary prey was the Fence degu-rat, and secondarily Bennett's chinchilla-rat and Darwin's leaf-eared mouse. Jaksic *et al.* (1992) reported similar findings for the same predators in Aucó, except that in this latter site, consumption of both Olivaceous field-mouse and Llaca mouse-opossum was higher than in Fray Jorge.

Only three previous studies of predator diets have been conducted in Fray Jorge. Fulk (1976) documented the diet of the Common Barn Owl between August 1972 and May 1973 as consisting mainly of Darwin's leaf-eared mouse (49% by number, n = 292), which is in line with our own results (Tables 3, 6). The next most frequent prey was Olivaceous field-mouse (34%), with Bennett's chinchilla-rat ranking fourth in numerical frequency in the diet (4%). Our results (Table 6) differ in that Bennett's chinchilla-rat (and sometimes also Fence degu-rat) was more often preyed upon than was Olivaceous field-mouse. Meserve *et al.* (1987) reported the winter diet (June 1985) of Burrowing Owls and Colpeo foxes: Fence degu-rat was the most frequent prey of both (35%, n = 17, and 74%, n = 50, respectively), and Darwin's leaf-eared mouse accounted for 18% and 0% of their prey, respectively. Our results for Burrowing Owls in the winters 1989-1990 (Tables 3, 4) do not agree well with their figures, but abundances of Fence degu-rat may have been much higher then, following a relatively high rainfall year. Our results for foxes during those winters concur better with Meserve *et al.* (1987), although in our study (Tables 3, 7) they also preyed extensively on Bennett's chinchilla-rat. The third previous study on a local predator is that by Mellado (1982) on the Chilean racerunner. Unfortunately, we did not collect data on

this species (see Castro *et. al.* 1991 for results from Aucó). In light of these comparisons, our dietary characterizations of Fray Jorge predators agree well, but some between-year and between-site (cf. Aucó) differences are apparent.

Diet breadths did not consistently increase during periods of low mammal abundance, as expected from optimal foraging arguments (Steenhof & Kochert 1988). Burrowing Owls and Colpeo foxes demonstrated the expected trend between high and low mammal seasons of 1990 but not during the preceding year, when they did not change or changed diet breadth in the opposite direction. Conversely, Common Barn Owls increased their diet breadth during the low mammal season of 1989, but failed to do so the following year (when they showed the opposite trend). Great Horned Owls, however, consistently increased their diet breadth during the low mammal seasons of both years. As stated above, rather than adult owls consuming a greater variety of prey items, it appeared that juvenile owls were responsible for the increased consumption of insects and arachnids. It thus appears that the local predators did not generally fit optimal foraging expectations, contrary to what was shown for three raptor species in Idaho (Steenhof & Kochert 1988).

Predator selectivity and lack of functional response by predators

Although Burrowing Owls were seen both day and night (Table 8), it appeared to us that they hunted for mammals primarily during the nocturnal period. This may account for the essentially diurnal Fence degu-rat not being selected by Burrowing Owls. Adult Fence degu-rat, in addition, is beyond the handling capability of these owls (Jaksic & Marti 1981; Schlatter *et al.* 1980). Indeed, Meserve *et al.* (1987) noted that most individuals of Fence degu-rat consumed by Burrowing Owls were juveniles or smaller subadults. Two of the highly selected prey, Darwin's leaf-eared mouse and Bennett's chinchilla-rat were nocturnal. It is noteworthy that all prey individuals of the latter species (the largest at the site) were juveniles. The continuously active Olivaceous field-mouse was the only other species that appeared to have been taken by Burrowing

TABLE 8

Summary of apparent prey preferences for predators at the study site. Symbols:
+ = taken more frequently than expected from trapping data; - = taken less frequently;
0 = taken about as expected; ? = taken erratically. Activity periods are: D = Diurnal;
C = Crepuscular; N = Nocturnal; DCN = Continuously active

Resumen de las aparentes preferencias de presas por los predadores en el sitio de estudio. Símbolos:
+ = consumido más de lo esperado por su abundancia en los trampeos; - = consumido menos de lo esperado;
0 = consumido tal cual esperado; ? = consumido erráticamente. Los períodos de actividad son D = diurno;
C = crepuscular; N = nocturno; DCN = activo día y noche

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

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

Owls more than expected from its field abundance.

The diurnality of the Fence degu-rat likely precluded its being selected by the strictly nocturnal Great Horned Owls (Table 8). The only selected prey were Darwin's leaf-eared mouse and Bennett's chinchilla-rat, which were nocturnal and the largest available during that time period. All mammalian prey species at the site were well within the handling capabilities of Great Horned Owls (Jaksic & Marti 1984).

Similar reasons as those posed above for Great Horned Owls may explain the prey selection pattern observed in Common Barn Owls (Table 8). In this case, however, adult Bennett's chinchilla rats were at about the upper size threshold for prey that can be successfully handled by the nocturnally hunting Common Barn Owl (Herrera & Jaksic 1980, Jaksic et al. 1982).

Colpeo foxes clearly selected the two largest rodents at the site, Fence degu-rat and Bennett's chinchilla-rat (Table 8). Given that the former prey is diurnal and the latter is nocturnal, this points to the foxes hunting both day and night, perhaps keying on large-sized prey (Jaksic et al. 1980; Jaksic 1989b). Indeed, it was very common to see them during daytime at the study site. Why the remaining five species were not taken at least in proportion to their field abundance is puzzling. None of these species was too small to be energetically unprofitable, and foxes ate much smaller-sized prey such as insects.

In summary, all three owls at the study site behaved similarly in terms of prey preferences, selecting the nocturnal Bennett's chinchilla-rat and Darwin's leaf-eared mouse, and underconsuming the remaining five species (except for Burrowing Owls, which in addition apparently selected the continuously active Olivaceous field-mouse). Foxes also selected Bennett's chinchilla-rat, but contrary to all three owls, they also selected the diurnal Fence degu-rat; the remaining five species were underconsumed by foxes. It appears, then, that only Bennett's chinchilla-rat was a "preferred" prey of all local predators, whereas Darwin's leaf-eared mouse was "preferred" prey of owls only, and Fence degu-rat of foxes only.

In no case was prey switching observed among predators. The local predators showed distinct prey "preferences" that were maintained throughout the study period. One factor contributing to this phenomenon was the constancy observed in most mammal species to covary in abundance through low and high seasons. As a consequence, the relative frequency with which "preferred" prey was encountered relative to "alternative" prey did not change through time, thus hampering the

formation of a new search image for predators (Murdoch 1969). Another contributing factor is that the four predators have been found in other studies to be extremely consistent in their prey selection through time. Iriarte *et al.* (1989) showed that this was the case for Colpeo foxes in the evergreen scrub of San Carlos, and Jaksic *et al.* (1992) showed the same in their concurrent study at Aucó, which included the same four predators. This latter case is interesting, because during that study a mammal irruption occurred (Jiménez *et al.* 1992), which involved primarily Darwin's leaf-eared mouse, Olivaceous field-mouse, and Llaca mouse-opossum, all species found in Fray Jorge as well. Despite these three species shooting up and then declining to crash densities of about 7% their peak, no predator seemed to take advantage of this prey surplus by switching preferences to these three temporarily superabundant species (Jaksic *et al.* 1992). If prey switching did not occur even under these extraordinary circumstances, much less would be expected in Fray Jorge. Why Chilean predators are so constant in their prey selection is an open question.

Predation impact on small mammals

Most predation on local small mammals seemed to be effected by Great Horned Owls, Common Barn Owls, and Colpeo foxes. Burrowing Owls may be comparatively inconsequential due to their pronounced insectivory and their modest abundance at the study site (Jaksic, pers. obs.). A similar explanation may apply to the insectivorous Chimango Caracaras and Chilean racerunners. In addition, the latter species has a limited activity season because it is ectothermic. This also applies to Long-tailed snakes, which in addition may need no more than thirty-two 30-g rodents to survive and reproduce successfully over a whole year (Bozinovic & Rosenmann 1988). Black-chested Eagles are important mammal predators elsewhere, but were only seen traversing (not hunting) over the study site.

Based on their food habits and selectivities, it may be speculated that the exclusion of owls from the study site should result in a population increase of chiefly Bennett's chinchilla-rat and Darwin's leaf-eared mouse, and that the exclusion of foxes should instead result

in an increase of both Bennett's chinchilla-rat and Fence degu-rat. We would not expect any major effect of predator exclusions on the remaining rodent species, which were taken less than expected from their field abundances. This speculation does not consider, however, other direct (e.g. competition) or indirect (e.g. competitive mutualism) interactions among the small mammals considered.

Comparison with other studies

Patterns of functional (i.e. prey switching) and numerical responses to changes in prey abundance have been previously reported in several studies of vertebrate predators and mammalian prey. Pearson (1964, 1966, 1971, 1985) showed that mammalian carnivores in California continued consuming their "preferred" prey, the California vole (*Microtus californicus*), even when it reached very low densities. He detected neither functional nor numerical responses of the predators, even when voles experienced dramatic cycles of abundance. In Idaho, Steenhof & Kochert (1988) found that both Golden Eagles (*Aquila chrysaetos*) and Prairie Falcons (*Falco mexicanus*) maintained strong preferences for jack rabbits (*Lepus californicus*) and ground squirrels (*Spermophilus townsendii*), respectively, despite marked changes in densities of those prey. However, Red-tailed Hawks (*Buteo jamaicensis*) did shift from ground squirrels to alternative prey when the former crashed. These authors did not report whether the raptors responded numerically to prey fluctuations. In central Sweden, Angelstam *et al.* (1984) documented strong functional responses of nine vertebrate predators to cyclic fluctuations of their main prey, the voles *Microtus agrestis* and *Clethrionomys glareolus*. However, no numerical responses were reported. In southern Sweden, Erlinge *et al.* (1982, 1983, 1984) noted both numerical and functional responses of vertebrate predators (too numerous to mention here) to cyclic changes in vole density. Here, resident generalist predators showed no numerical but strong functional responses, whereas nomadic specialist predators showed the opposite trend. In western Finland, Korpimäki & Norrdahl (1991) reported marked numerical responses by three apparently nomadic raptors (*Falco tinnuncu-*

lus, *Asio flammeus*, and *Asio otus)*, but no clear functional responses. In central Australia, Corbett & Newsome (1987) reported that dingos (*Canis familiaris dingo*) preyed consistently on rabbits (*Oryctolagus cuniculus*) throughout a prolonged drought period, and displayed a modest functional response, but not a numerical one. In southern Australia, however, Sinclair *et al.* (1990) noted both functional and numerical responses of predators (*Elanus notatus, Haliastur sphenurus, Falco cenchroides, Falco berigora, Accipiter fasciatus, Ninox boobook, Vulpes vulpes*, and *Felis catus*) to irruptions of house mouse (*Mus domesticus*). In north-central Chile, Jaksic *et al.* (1992) reported that Burrowing, Great Horned, Austral Pygmy, and Common Barn Owls, together with Colpeo and Grey foxes, displayed different selectivities among themselves, but maintained them despite the occurrence of a small-mammal outbreak and the ensuing crash. They noted strong numerical responses, but a lack of functional shifts in diet.

It appears, then, that numerical and functional responses are uncoupled components of vertebrate predation on small mammals. They may be both present (southern Sweden, southern Australia), both absent (California, central Australia, this study, perhaps Idaho), or only one present (central Sweden, western Finland, north-central Chile). It is interesting that this may be so, even where prey species irrupt and crash, or experience long declines from normal densities (all studies except this). Perhaps the failure of vertebrate predators to respond both numerically and functionally accounts for their inability to determine the abundance of mammal populations, as shown by Pearson (1964), Erlinge *et al.* (1984), Sinclair *et al.* (1990), and Jaksic *et al.* (1992), from different parts of the world. However, as exemplified by the study of Sinclair *et al.* (1990), the simultaneous occurrence of both numerical and functional responses seems to be a necessary, but not a sufficient condition, for vertebrate predators to become effective agents in the determination of mammalian abundance. This does not mean that the same predators must display both responses, but (as demonstrated by Hanski *et al.* 1991, on modelling grounds) that a combination of numerical- and functional-responders may

contribute to such determination of prey numbers.

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