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NUMERICAL AND FUNCTIONAL RESPONSE OF BURROWING OWLS TO LONG-TERM MAMMAL FLUCTUATIONS IN CHILE

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ABSTRACT.—Most studies to date indicate that the burrowing owl (*Speotyto cunicularia*) is a generalist species that eats variable combinations of vertebrates and invertebrates, mainly small mammals and insects. These combinations vary through time, and thus the burrowing owl has been labeled a seasonally opportunist species. However, because of the numerically higher incidence of insects in its diet, this species has been ascribed to insectivorous trophic guilds. We found that burrowing owls in mediterranean Chile: (1) consistently consumed more invertebrates than vertebrates but the biomass contribution of these two categories was the reverse, (2) co-varied in number of resident individuals with the density of small mammals in the field, (3) decreased the casting of pellets with insects as mammal densities increased, and (4) increased the frequency of mammals in the diet as the latter increased in the field. We propose that Chilean burrowing owls displayed both numerical and functional responses to the abundance of local small mammals, thus suggesting that they depended more heavily on this prey type than on insects. Perhaps Chilean burrowing owls should be classified trophically as carnivorous instead of as insectivorous predators.

KEY WORDS: *burrowing owl*; *Chile*; *functional response*; *mammal fluctuation*; *numerical response*; Speotyto cunnicularia.

Respuesta numérica y funcional de pequenes ante fluctuaciones de largo plazo de micromamíferos en Chile

RESUMEN.—La mayoría de los estudios a la fecha indican que la lechucita cavadora (*Speotyto cunicularia*) es una especie generalista que come combinaciones variables de vertebrados e invertebrados, principalmente de micromamíferos e insectos. Estas combinaciones varían en el tiempo y es así como la lechucita cavadora se ha considerado como una especie estacionalmente oportunista. Sin embargo, debido a la mayor incidencia numérica de los insectos en su dieta, esta especie ha sido adscrita a gremios tróficos insectívoros. Nosotros encontramos que lechucitas cavadoras en Chile mediterráneo: (1) consistentemente consumían más invertebrados que vertebrados, pero la contribución de biomasa de estas dos categorías era la inversa, (2) co-variaban en número de individuos residentes, con la densidad de micromamíferos en el terreno, (3) disminuían el número de egagrópilas con insectos a medida que aumentaban las densidades de micromamíferos, y (4) incrementaban la frecuencia de mamíferos en la dieta a medida que estos últimos aumentaban en el terreno. Proponemos que las lechucitas cavadoras chilenas demuestran tanto respuestas numéricas como funcionales a la abundancia local de micromamíferos, sugiriendo así que ellas dependen más fuertemente de este tipo de presas que de los insectos. Quizás las lechucitas cavadoras chilenas debieran ser categorizadas tróficamente como depredadores carnívoros en vez de insectívoros.

[Traducción Autores]

The burrowing owl (*Speotyto cunicularia*) is distributed from southern Canada to the United States (with isolated populations in Florida and the Caribbean Archipelago) all the way through Central and South America, wherever adequate habitats are found. The burrowing owl inhabits open areas such as deserts and sparse shrublands, and although it is active throughout the day, its peak of activity occurs at crepuscular hours. It is a sit-and-wait predator that infrequently hunts on the wing (Burton 1973). The food habits of the burrowing owl are relatively well-known (Marti et al. 1993), although information from South America is more scanty. Only the Pampean region of Argentina (e.g., Bellocq 1987, 1988) and the Mediterranean region of Chile (Jaksić and Marti 1981, Jaksić et al. 1992, 1993a) seem well-studied with regard to the diet of this owl. Nevertheless, all studies indicate that the burrowing owl is apparently a generalist species that eats variable combinations of vertebrates and invertebrates, mainly small mammals and insects.

In mediterranean Chile, both short- and long-term studies (Schlatter et al. 1980, Meserve et al. 1987, Torres-Contreras et al. 1994) indicate that the burrowing owl is more of a specialist on small mammals during the breeding season, and a generalist that preys more frequently on insects during the wintering season. Indeed, Jaksić and Marti (1981) and Jaksić (1988) have labeled this owl as a seasonally opportunist species. Consequently, its trophic role in predator assemblages appears to differ according to the season the corresponding study was undertaken. For instance, Jaksić et al. (1981) considered the burrowing owl to be insectivorous-carnivorous (in that sequence), Jaksić and Delibes (1987) ascribed it to an insectivorous trophic guild, whereas Jaksić et al. (1993b) ascribed it to an omnivorous (invertebrates plus vertebrates) guild. However, all of the Chilean studies cited above have analyzed the burrowing owl diet only in terms of prey numbers, not prey biomass (unlike the case in Argentina; see Bellocq 1987, 1988).

Here, we report a 3-yr study of the burrowing owl in mediterranean Chile, and analyze the numeric and biomass contribution of both vertebrate and invertebrates to its diet. We found that the burrowing owl depends heavily on small mammal biomass rather than on that of invertebrates, and that, in fact, small mammal consumption and owl numbers follow very closely small mammal availability at our study site in northcentral Chile.

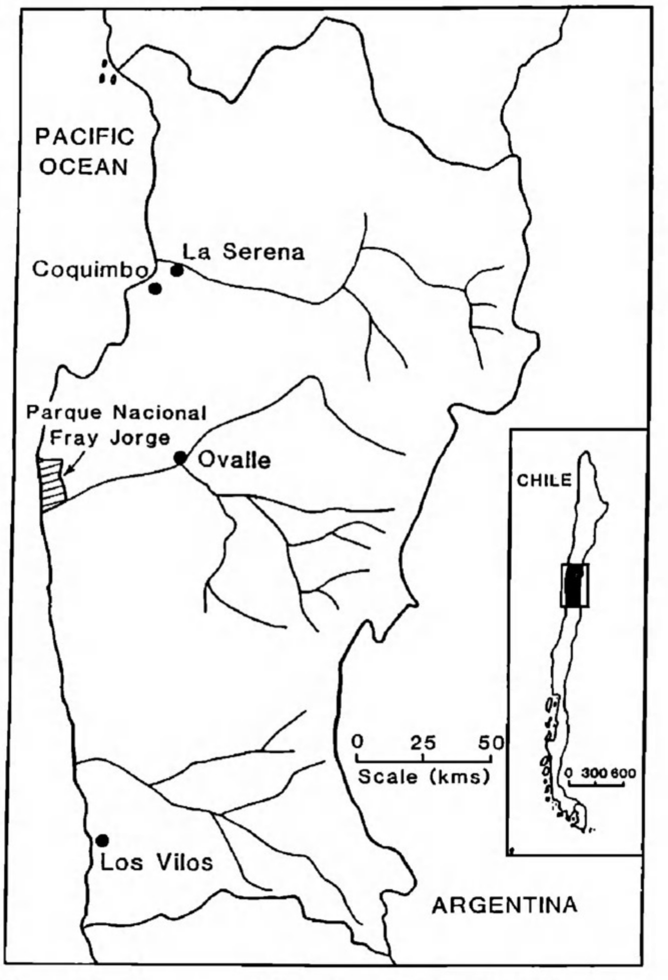

Figure 1. Location of Fray Jorge National Park, northcentral Chile.

MATERIAL AND METHODS

The study area is located in Fray Jorge National Park (30°38'S, 71°40'W), 400 km north of Santiago, Chile (Fig. 1) The park is near the Pacific coastline, and comprises 10 000 ha of arid mediterranean thorn-scrub vegetation, and some remnants of fog forest at higher elevations along the coastal range (Meserve and Le Boulengé 1987). Mean annual precipitation is 85 mm, and occurs mostly (90%) during the austral winter (May to September). Summer is warm and dry, although frequent fog contributes to high relative humidity. Work took place from September 1990 to August 1993 in "Quebrada de las Vacas," a broad valley with relatively homogeneous vegetation, dominated by drought-deciduous and evergreen shrubs (59% cover), including *Porlieria chilensis, Adesmia bedwellii,* and *Proustia pungens* (Gutiérrez et al. 1993).

We made monthly counts of burrowing owls and collected their pellets from three burrows, also on a monthly basis. We followed standard procedures of raptor diet analysis (Marti 1987), and were able to identify most vertebrates to the species level. Our taxonomic resolution for invertebrates ranged from order to species. The minimum number of individuals contained in each pellet was determined according to the number of single (e.g., stings, crania) or paired (e.g., elytra, eyes) anatomical elements detected under a stereoscope. Simultaneously with this study, we made monthly assessments of the minimum number of small mammals known to be alive in four 0.56-ha livetrapping grids (see details in Meserve et al. 1993).

Prey categories used for biomass assessments in burrowing owl diet were species of small mammals, classes

Table 1. Number of prey (and their respective weights) in the diet of burrowing owls in Fray Jorge National Park in the six biological seasons of the study (B = breeding season, W = wintering season).

PREY ITEMS	MASS (g)	B90	W91	B91	W92	B92	W93	TOTAL
Marsupialia								
Marmosa elegans	23	3	0	0	3	10	0	16
Rodentia unidentified	75	8	17	7	11	18	6	67
Cricetidae unidentified	43	25	3	0	9	25	19	81
Phyllotis darwini	58	6	5	4	8	69	95	187
Oryzomys longicaudatus	24	5	0	0	15	6	1	27
Akodon olivaceus	32	4	0	2	8	21	16	51
Akodon longipilis	54	0	0	0	0	0	1	1
Akodon unidentified	43	0	0	1	0	0	0	1
Octodontidae								
Octodon degus	141	0	1	1	0	3	4	9
Abrocomidae								
Abrocoma bennetti	201	11	0	0	1	1	0	13
Total mammals		62	26	15	55	153	142	453
Birds unidentified	20	0	17	11	4	0	0	32
Passeriformes unidentified	20	25	0	0	0	0	0	25
Total birds		25	17	11	4	0	0	57
Amphibia								
Bufo chilensis	5	0	1	0	0	0	0	1
Total amphibians		0	1	0	0	0	0	1
Reptilia								
Philodryas chamissonis	80	1	0	0	0	0	0	1
Total Reptilia		1	0	0	0	0	0	1
Insecta								
Coleoptera unidentified	1	29	155	7	7	5	4	207
Tenebrionidae unidentified	1	297	83	1	0	0	0	381
Nycterinus sp.	1	166	166	39	30	34	21	456
Praocis sp.	1	36	308	27	70	120	40	601
Gyriosomus sp.	1	5	0	8	0	1	0	14
Auladera sp.	1	13	3	1	0	1	2	20
Scotobius sp.	1	3	6	1	0	2	1	13
Diastoleus sp.	1	19	7	7	1	0	0	34
Scarabaeidae unidentified	1	151	51	34	27	30	24	317
Trox sp.	1	0	5	0	0	0	0	5
Buprestidae unidentified	1	0	0	2	0	0	0	2
Ectinogonia buqueti	1	4	0	0	0	0	0	4
Carabidae unidentified	1	10	51	4	9	7	10	91
Calosoma vagans	1	0	4	2	0	0	0	6
Curculionidae unidentified	1	100	81	26	13	10	9	239
Hymenoptera unidentified	1	3	0	4	2	0	0	9
Pompilidae unidentified	1	0	1	2	2	0	0	5
Formicidae unidentified	1	0	132	10	5	0	10	157
Orthoptera unidentified	1	15	1	0	0	0	0	16
Gryllidae unidentified	1	0	0	0	0	0	4	4
Acrididae unidentified	1	0	0	12	12	0	0	24
Lepidoptera unidentified	1	0	3	0	0	0	0	3
Larva unidentified	1	12	0	0	0	0	0	12
Total insects		863	1057	187	178	210	125	2620

Table 1. Continued.

PREY ITEMS	MASS (g)	B90	W91	B91	W92	B92	W93	TOTAL
Arachnida								
Scorpionida unidentified	1	285	90	38	33	30	25	501
Aranea unidentified	1	374	10	11	3	0	0	398
Opilionida unidentified	1	2	1	0	0	0	0	3
Total arachnids		661	101	49	36	30	25	902
Total prey		1612	1202	262	273	393	292	4034
Total pellets		173	82	32	58	144	138	627

of other vertebrates, and classes of arthropods. Biomass of different small mammal species from the same study site were reported by Meserve et al. (1987). In the case of unidentified cricetids and unidentified rodents (either cricetid or caviomorph), we assigned them the arithmetic mean mass of the different cricetids or rodents identified in the diet. For avian, reptilian, and amphibian prey in the diet we estimated (based on field experience) the following mean masses: 20, 80, and 5 g, respectively. For arthropods we arbitrarily assigned (and likely overestimated) a mean mass of 1 g.

Because monthly assessments of diet or of small mammal abundance are not independent from preceding or subsequent months, and because calendar seasons were meaningless regarding these assessments, we chose to perform our analysis using biologically meaningful seasons (see Castro and Jaksić 1995, for justification): breeding (September through February) and wintering (March through August). Although we lose quite a number of degrees of freedom for statistical analyses (i.e., 12 mo are pooled into only two seasons), and thus all of our tests are rendered conservative, we preferred to err on the safe side.

RESULTS AND DISCUSSION

Arthropods (primarily insects, secondarily arachnids) were the numerically most frequent prey in the diet of burrowing owls, accounting for as high as 96% (wintering 1991) to as low as 51% (wintering 1993) of individual prey in the diet. Small mammals numerically accounted for between 2% (wintering 1991) and 48% of prey items (wintering 1993). Other vertebrates (birds, reptiles, and amphibians) never exceeded 4% of individual prey in the diet (Table 1).

When the above results were converted into biomass equivalents, the percentages reversed (Fig. 2), with small mammals accounting for most of the biomass consumed by burrowing owls (1–7 kg/season) and arthropods always accounting for less than 2 kg. The biomass representation of small mammals in the diet of burrowing owls as well as their numerical abundance followed quite closely the variations in density of small mammals at the site (Fig. 2, see numerical details in Table 2). It thus seems that burrowing owls display a numerical response to the abundance of small mammals. Because we did not assess the abundance of insects in the field, we cannot determine whether these owls also responded numerically to insect abundance. This seems unlikely, however, as insect and small mammal prey fluctuated in phase (S.I. Silva pers. obs.).

The correlation between percentage of burrowing owl pellets with arthropod contents and small mammal density was significantly negative (Fig. 3). It was also negative when calculated between percent arthropod number or biomass in the diet and mammal abundance in the field ($r_s = -0.94$, $N = 6$, $P = 0.035$ for both correlations). It appears, then, that burrowing owls consumed fewer arthropods when more small mammals were available in the field, and

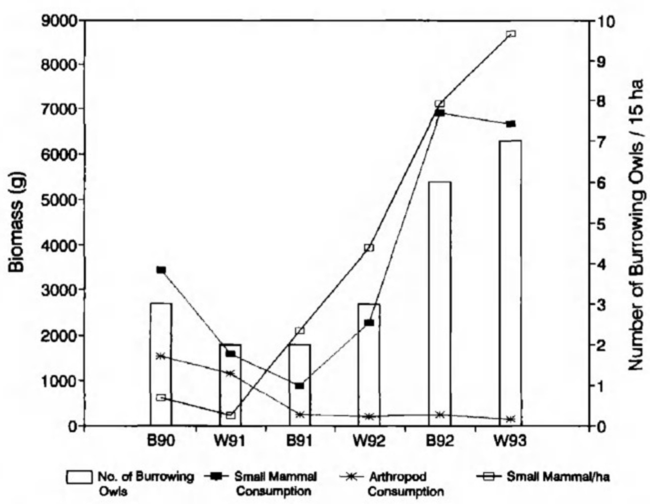

Figure 2. Biomass of small mammals and insects estimated from pellet contents of burrowing owls in Fray Jorge National Park, in the six biological seasons of the study (B = breeding season, W = wintering season). Also depicted is the abundance of burrowing owls in the study site, as well as the trend in small mammal density, from data in Table 2.

Table 2. Density of small mammals (*N*/ha) in Fray Jorge National Park in the six biological seasons of the study (B = breeding season, W = wintering season). Tabular entries are means of six monthly assessments made in four 0 56-ha live-trapping grids.

SPECIES	B90	W91	B91	W92	B92	W93
Marmosa elegans	0.58	0.33	1.93	3.75	1.75	1.67
Phyllotis darwini	3.46	0.92	11.21	19.83	28.96	31.96
Oryzomys longicaudatus	0.00	0.00	6.93	19.25	1.75	1.29
Akodon olivaceus	0.38	0.17	32.96	45.00	59.96	35.71
Akodon longipilis	0.00	0.00	2.71	8.71	11.21	12.58
Abrocoma bennetti	0.38	0.04	0.29	0.13	1.54	1.71
Octodon degus	3.00	1.29	2.21	5.83	26.46	42.67
Total (*N*/ha)	7.79	2.75	58.25	102.50	131.63	127.58
Range (*N*/ha; 6 mo)	5.5–9.0	0.0–7.0	3.0–106.0	90.3–112.8	92.5–161.3	101.5–147.5
N Burrowing Owls present	3	2	2	3	6	7

vice versa. If the percentage of pellets with insects over time were considered as the variation in the diet of a representative individual of burrowing owl, then owls at our study site may be said to display a functional response to the abundance of small mammals. Indeed, the percentage of mammal prey by number and biomass in the diet was positively correlated with small mammal abundance in the field ($r_s = 0.94$, $N = 6$, $P = 0.035$ for both correlations).

Thus, judging by numbers it is correct to state that burrowing owls in our study site were generalists (in the sense that they consume both vertebrates and invertebrates) or seasonally facultative (sometimes heavily insectivorous, others strongly carnivorous). However, judging by prey biomass, it is clear that burrowing owls were always more dependent on small mammals than they were on arthropods, whose contribution to the diet was negligible when small mammal abundance exceeded 100 individuals/ha (Fig. 3). Densities above that threshold were measured at the site in three out of the six seasons of the study (Table 2).

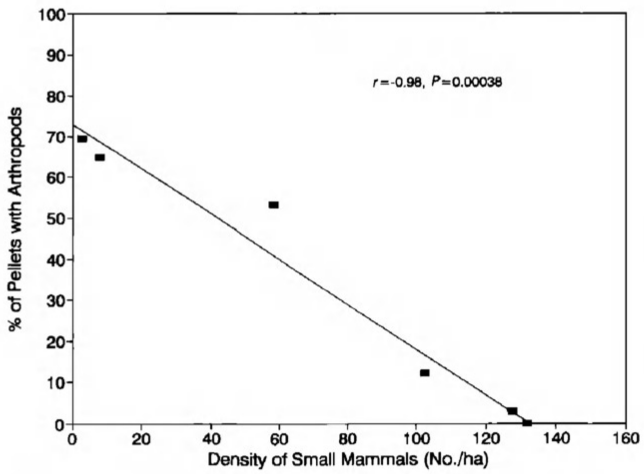

Figure 3. Percentage of burrowing owl pellets containing insects versus small mammal density in Fray Jorge National Park, as reported in Table 2. Each data point represents a biological season (breeding or wintering). The regression line is drawn only to emphasize the trend observed.

Finally, demonstration that burrowing owls at the study site displayed both numerical and functional responses to the abundance of small mammals, suggests that they depended more heavily on this prey than on arthropods. Perhaps Chilean burrowing owls should be classified trophically as carnivorous instead of as insectivorous predators.

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