FEEDING ECOLOGY OF THE BARN OWL IN CENTRAL CHILE AND SOUTHERN SPAIN: A COMPARATIVE STUDY

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ABSTRACT.—We examined the food habits of the Barn Owl (*Tyto alba*) in the mediterranean-climate areas of central Chile and southern Spain. In both areas most prey were small mammals (95% and 87% in Chile and Spain, respectively). Spanish Barn Owls frequently fed on reptiles and amphibians (4.5% of the diet), whereas such prey were not consumed by Chilean Barn Owls. The most noticeable difference involved mean body weight of small mammal prey (70.7 g in Chile vs. 21.2 g in Spain), which was associated with the different weight ranges of small mammals present in the two areas (40–320 g in Chile vs. 2.5–390 g in Spain). The narrower diet and specialization on mammals by Chilean Barn Owls was probably accounted for by the greater availability of larger small mammals and also perhaps by their greater overall density. In spite of the different prey weights taken by the owls, their body weights were similar in the two areas. These results are discussed in relation to the species configuration of the owl communities in Chile and Spain. *Received 1 February 1980, accepted 14 April 1980.*

MUCH information has been published on the diet of the Barn Owl (*Tyto alba*) in different parts of the world (Clark et al. 1978). Recently, its food habits have been documented in central Chile and southern Spain (Jaksić and Yáñez 1979, Herrera 1973, respectively). These are areas of very similar climate, physiognomy, and resources, characterized by the presence of a chaparral-like shrub vegetation (di Castri and Mooney 1973). By comparing the diet of the Barn Owl in these two distant but nevertheless similar areas, we expect to gain some insight into the ecological factors that may affect its food habits in different parts of its range.

STUDY AREAS AND METHODS

The diet composition of Barn Owls in central Chile was obtained by pooling data reported by Reise (1970), Schamberger and Fulk (1974), Fulk (1976), and Jaksić and Yáñez (1979) and unpublished material kindly provided by D. Torres. The largest part of southern Spanish data were taken from Herrera (1973); unpublished information from a few supplementary localities was added. All these data were combined to form a single sample for each region. Both study areas fall clearly within the limits of the mediterranean-type climate (di Castri and Mooney 1973), with dry-hot summers and rainy-mild winters.

For central Chile, 3,594 prey items were identified in 2,545 pellets from 18 localities enclosed in a geographical area between latitudes 30°30′–34°36′S and longitudes 70°31′–71°40′W. The vegetation of the entire region, disregarding agricultural lands, is that of typical central Chilean scrubland (chaparral), an assemblage of shrubby species described in Thrower and Bradbury (1977). Habitat types where we sampled pellets were generally moderately to slightly disturbed by human activities. About 15% of the pellets, however, were deposited near areas of intense agricultural practice. Spanish food data, totaling 14,407 prey items in nearly 3,500 pellets, came from 26 localities fairly evenly distributed between latitudes 36°30′–38°30′N and longitudes 4°–7°W. Various habitat types are represented in this area, ranging from arable land in the bottom of large valleys to fairly undisturbed evergreen oak woodlands (*Quercus ilex*) and schlerophyllous shrublands in mountain and hill areas. These latter habitat types were the best represented in terms of number of prey items; hence, the diet composition of Spanish Barn Owls should be representative of individuals occupying habitats subjected to moderate or little human influence.

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TABLE 1. Gross diet composition of the Barn Owl in central Chile and southern Spain. Trophic diversity (H'NGG) and evenness (JNGG) in relation to the number of prey items contributed by each higher taxonomic category are also shown. N = number of prey items.

	Central Chile		Southern Spain	
Prey type	N	%	N	%
Mammals	3,417	95.1	12,492	86.7
Birds	130	3.6	590	4.1
Reptiles	—	—	121	0.8
Amphibians	—	—	539	3.7
Invertebrates	47	1.3	665	4.6
H'NGG	0.22		0.56	
JNGG	0.14		0.35	

In addition to computing the dietary percentage of different prey categories in the two areas, we further characterized Barn Owl food habits by the following parameters: (1) MWSM, mean weight of small mammals in the diet, which is the grand mean obtained by summing the products of the numbers of individual prey times their weight (g) and dividing by the total number of mammalian prey in the sample. Mean weights of adult small mammals in central Chile were reported by Schlatter, Toro, Yáñez, and Jaksić (1980) and Schlatter, Yáñez, Núñez, and Jaksić (1980); mean weights of adult small mammals in southern Spain were obtained from van der Brink (1968) and the mammal collection of Estación Biológica de Doñana, as detailed in Herrera (1973). (2) H'NGG, trophic diversity in relation to the number of individuals contributed by each higher taxonomic unit (mammals, birds, reptiles, amphibians, invertebrates). (3) H'NM, trophic diversity in relation to the small mammal component of the diet (rodents, lagomorphs, insectivores, marsupials, chiropterans). The latter two parameters were computed by means of the Shannon's information function as described in Herrera (1974); corresponding values of evenness ($J = H'/H'\max$) were also obtained.

Weight and wing length data for sympatric owl species in central Chile were taken from the ornithological collections of the Museo Nacional de Historia Natural (Santiago), Instituto Central de Biología de la Universidad de Concepción, Museo de Historia Natural de Valparaíso, and Instituto de Zoología de la Universidad Austral (Valdivia). All data for southern Spain were from skins preserved in the collection of Estación Biológica de Doñana unless otherwise stated.

RESULTS

General composition of the diet.—Small mammals were the main prey of Barn Owls in both central Chile and southern Spain (Table 1), accounting for nearly 95% and 87% of total prey items, respectively. Reptiles and amphibians were absent from the diet of Chilean Barn Owls, whereas these two groups made up 4.5% of all prey items in southern Spain. The importance of bird prey was similar in both regions, while invertebrates were represented more frequently in southern Spain than in central Chile (4.6% vs. 1.3%, respectively).

Among mammals (excluding chiropterans), the importance of rodents in the diet of Barn Owls was greater in Chile than in southern Spain (95.5% vs. 77.5%), where insectivores contributed an important fraction of the prey (22.5%; see Table 2). This latter group is not present in Chile. The only prey species found in both regions are the cosmopolitan house mouse (*Mus musculus*), Norway rat (*Rattus norvegicus*), black rat (*R. rattus*), and European rabbit (*Oryctolagus cuniculus*), this latter only recently introduced to central Chile (Jaksić et al. 1979). Norway rats and European rabbits were rarely consumed by the Barn Owl in either Chile or Spain; this is probably related to the large size of both species (see Table 2), as the specimens found in pellets were juveniles. Black rats appear more frequently in the diet of Chilean than in that of Spanish Barn Owls (6.8% vs. 0.6%), and the reverse is true for the house mouse (7.3% vs. 47.4% of total prey in Chile and Spain, respectively).

TABLE 2. Composition of the small mammal component of the diet of the Barn Owl in central Chile and southern Spain. Trophic diversity (H'NM) and evenness (JNM) in relation to the small prey are also shown. *N* = number of prey items. MWSM = mean weight of small mammal prey ± standard deviation; this figure is calculated on the basis of all small mammals with known weight; rabbits are computed as juveniles.

Prey species	Central Chile			Southern Spain		
	N	%	Weight (g)	*N*	%	Weight (g)
RODENTIA	*3,237*	*95.5*	—	*9,572*	*77.5*	—
Abrocoma bennetti	134	4.0	219	—	—	—
Akodon longipilis	208	6.1	76	—	—	—
Akodon olivaceus	390	11.5	40	—	—	—
Apodemus sylvaticus	—	—	—	1,702	13.8	27.3
Arvicola sapidus	—	—	—	18	0.1	216.0
Eliomys quercinus	—	—	—	39	0.3	82.5
Mus musculus	248	7.3	17	5,857	47.4	20.0
Octodon degus	101	3.0	230	—	—	—
Oryzomys longicaudatus	939	27.7	45	—	—	—
Phyllotis darwini	958	28.3	66	—	—	—
Pitymys duodecimcostatus	—	—	—	1,861	15.1	27.5
Rattus norvegicus	1	<0.1	320	27	0.2	390.0
Rattus rattus	232	6.8	158	68	0.6	180.0
Spalacopus cyanus	26	0.8	112	—	—	—
LAGOMORPHA	*1*	*<0.1*	—	*5*	*<0.1*	—
Oryctolagus cuniculus[a]	1	<0.1	1,300	5	<0.1	1,100.0
MARSUPIALIA	*153*	*4.5*	—	—	—	—
Marmosa elegans	153	4.5	40	—	—	—
INSECTIVORA	—	—	—	*2,774*	*22.5*	—
Crocidura russula	—	—	—	2,371	19.2	6.6
Suncus etruscus	—	—	—	403	3.3	2.5
CHIROPTERA	*26*	—	—	*141*	—	—
Unidentified	26	—	—	141	—	—
H'NM		1.93			1.41	
JNM		0.78			0.61	
MWSM (g)		70.7 ± 52.3			21.2 ± 24.0	

[a] Juveniles (180 g in central Chile; 150 g in southern Spain).

Size of small mammal prey.—The mean body weight of small mammal prey (MWSM) differed greatly between the two regions (Table 2), the figure being more than three times greater in Chile ($P < 0.001$, weighted-variance t-test; see Sokal and Rohlf 1969). Because the largest prey taken in Chile and Spain were of equivalent size, the much smaller MWSM in Spain was, then, a consequence of the greater comsumption of low-weight insectivores and rodents there. The small house mouse (20 g, nearly 50% of total prey), particularly, affects substantially the MWSM value computed for Spanish Barn Owls. In central Chile, the smallest prey available was the house mouse (17 g), but it accounted for only 7.3% of the total diet. The most important prey types there were the leaf-eared mouse (*Phyllotis darwini*) and the rice rat (*Oryzomys longicaudatus*), with body weights of 66 g and 45 g, respectively. Together, they accounted for 56% of total prey.

For both central Chile and southern Spain, the small mammal species preyed upon by the Barn Owls corresponded to the spectrum of available prey in the two regions, disregarding some local, endemic taxa (Herrera 1973, 1974; Jaksić and Yáñez 1979). The large number of prey items and localities considered, together with information derived from extensive small mammal trapping in the two areas, support this contention. Hence, it is possible to analyze some characteristics of the

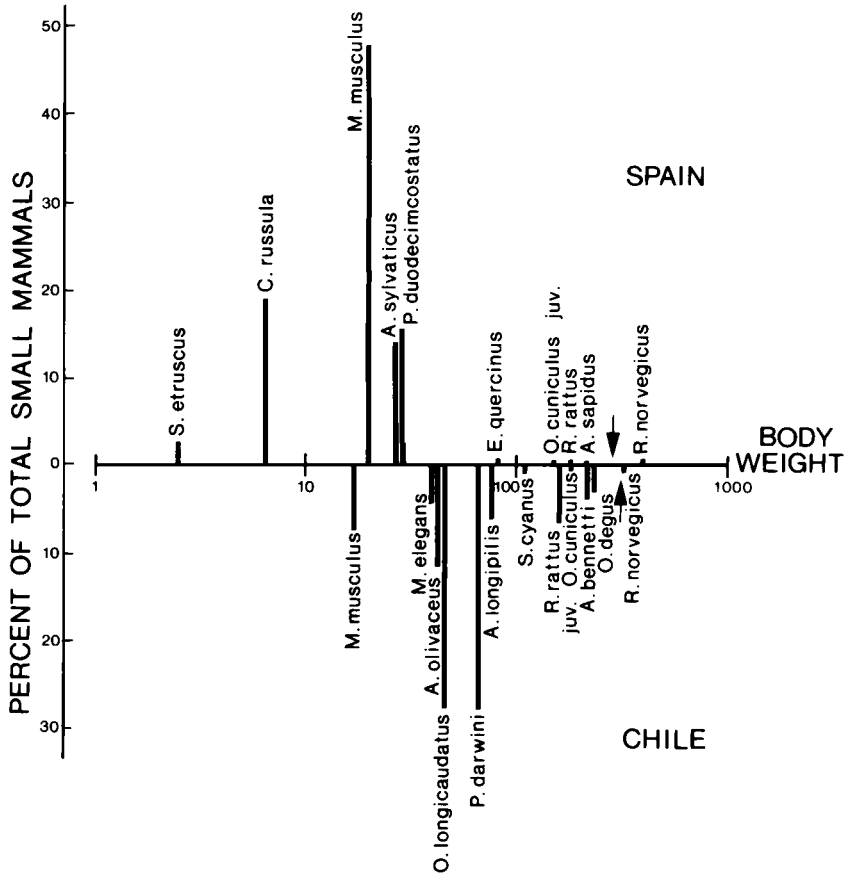

Fig. 1. Relative frequencies (%) of small mammal prey in the diet of Barn Owls in central Chile and southern Spain (excluding bats), ordered along a logarithmic axis of body weights. Arrows denote mean body weight of Barn Owls in the two areas (Table 3); generic names of small mammal species are shown in Table 2.

prey in central Chile and southern Spain on the basis of the sampling made by the Barn Owls. Ordering small mammal species along a gradient of body weight in both areas (Fig. 1), it is apparent that the Barn Owl faces very different situations in the two regions with regard to frequency distributions of available small mammal prey. In southern Spain there are two distinct groups of small mammals (2.5–27.5 g, and 82.5–390 g), with no species in the 30–80-g range. The "light" species group is totally lacking among Chilean small mammals (the cosmopolitan house mouse being the exception), whereas the "heavy" group is nearly as equally well represented as in Spain, largely by the same species. Most important, a group of four "medium" species (40–80 g) exists in central Chile, precisely in the gap of the Spanish weight distribution. It is clear, then, that the striking difference in the mean body weight of prey between the two regions can be attributed to the differential availability of prey-weights in both areas.

Trophic diversity.—The previous results show that Chilean Barn Owls have a narrower diet containing more mammalian prey than do their Spanish counterparts.

TABLE 3. Owl assemblages in central Chile and southern Spain. Owls from the two areas were primarily matched by taxonomic relatedness, secondarily by size similarity. Only resident species in typically mediterranean habitats were considered. Sample sizes for means are shown in parentheses; both sexes were combined. Difference in wing length between populations of the Barn owl in central Chile and southern Spain is statistically significant ($t = 6.29$, $P < 0.001$), but difference in body weight is not ($t = 1.58$, $P > 0.12$).

Central Chile			Southern Spain		
Owl species	Mean body weight (g)	Mean wing length (mm)	Owl Species	Mean body weight (g)	Mean wing length (mm)
Bubo virginianus	1,500 (2)	351 (17)	*Bubo bubo*	1,886 (8)	469 (14)
Asio flammeus	350 (2)	325 (19)	*Strix aluco*	426 (10)	263 (17)
Tyto alba	307 (8)	302 (16)	*Tyto alba*	281 (20)	283 (34)
Athene cunicularia	247 (3)	193 (25)	*Athene noctua*	148 (30)	157 (41)
Glaucidium brasilianum	74 (4)	108 (12)	*Otus scops*	69 (2)[a]	152 (2)[a]

[a] After Dementiev and Gladkov (1966); average of female and male means.

This is also apparent from a comparison of H'NGG values, which are more than two times higher in southern Spain; the same holds true for evenness values (Table 1). Consequently, the relative contribution of the various higher taxonomic categories to the Barn Owls' diet is more unequal in Chile than in Spain. The diversity and evenness of the small mammal component of the diet (H'NM) do not show as great a contrasting difference as in the previous case, although they are noticeably higher in central Chile. This means that the diet of Barn Owls in this latter area was based upon a more diverse array of small mammal species, which in addition were more equally represented (Table 2).

DISCUSSION

Our results reveal that the diets of the Barn Owl in central Chile and southern Spain differ in several important respects. Chilean Barn Owls concentrate more on small mammals, which tend to be larger than those preyed upon by Spanish Barn Owls. The latter more frequently include nonmammalian prey in their diet, and the diversity of small mammals consumed is less than in central Chile.

The trophic diversity for Chilean Barn Owls is intermediate between the very high H'NGG values shown by southwestern Spanish populations and the extremely low figures exhibited by populations in nonmediterranean, western European localities (Herrera 1974). In these latter areas the Barn Owls fed almost exclusively on an abundant supply of voles (*Microtus* spp.; see Uttendörfer 1939). Although of the same order of magnitude, the diversity of small mammals (H'NM) in the diet of Barn Owls in Chile was slightly lower than in temperate, western Europe, but was noticeably higher than in mediterranean Spain (Herrera 1974). The concurrent, opposite variation of H'NGG and H'NM values observed in western Europe has been interpreted as a response of the Barn Owl to changes in the abundance and density of small mammals, which become much lower in the mediterranean areas of southwestern Europe (Herrera 1974, Herrera and Hiraldo 1976). The same argument may also explain some Chile-Spain differences. Species diversity of small mammals appears to be similar in central Chile and southern Spain, but density is probably higher in central Chile. Schamberger and Fulk (1974) obtained figures of 0.06, 0.13, and 0.34 individuals/trap-night in three habitat types in central Chile,

and year-round trapping by Jaksić and Yáñez (1978) in the same general area gave a monthly average of 0.03 individuals/trap-night (range between 0.02 and 0.07). In southern Spain trapping success usually ranges between 0.00 and 0.04 individuals/trap-night, as revealed by several years of small mammal trapping in many habitat types and nearly 20 localities (R. C. Soriguer, unpubl.). These differences in small mammal densities, if substantiated by more detailed studies in the future, may partly explain the dissimilarities in trophic diversity between Chilean and Spanish Barn Owls. If Barn Owls forage in an optimal manner, greater small mammal density would theoretically favor a concentration of predation on this group, while discouraging predation upon other energetically less profitable types like reptiles, amphibians, and invertebrates (Schoener 1971, Pyke et al. 1977, Krebs 1978).

There are, however, two factors that complicate an acceptance of this explanation. These are the interregional differences in the size distribution of small mammal species and the configuration of the community of coexisting owl species. These two factors, together with the differences in small mammal density discussed above, most likely operate simultaneously to generate interregional dietary differences, but presently it is not possible to assess the relative importance of either of them.

As shown above, in southern Spain there are two distinct groups of small mammal species. The "heavy" group is shared with central Chile, and in both areas it represents a negligible fraction of total prey items (made up mostly of juvenile individuals). Species in this group are close to, or greater than, the body weight of the Barn Owl (Table 3 and Fig. 1) and presumably exceed its upper limit of handling capacity. If one disregards this set of heavy species, the Barn Owl is left with a group of "light" prey species in Spain and a group of "medium" species in Chile. Accordingly, the Chilean Barn Owls feed on mammalian prey of presumably higher energetic reward than their Spanish counterparts, provided that the body size of the owls is similar in both areas (Table 3) and assuming that pursuit and handling time of heavier Chilean small mammals is not disproportionately higher. Under these circumstances, in terms of optimal foraging theory (Pyke et al. 1977, Krebs 1978), it is not necessary to propose greater overall density of small mammals in central Chile to account for the narrower diet of Barn Owls there. An "average" Chilean small mammal is energetically more profitable than a Spanish one, relative to other alternative prey of smaller size (bird, reptile, amphibian, invertebrate). Therefore, the optimal diet of Chilean Barn Owls should contain fewer nonmammalian prey than the diet of Spanish Barn Owls, as it in fact does (Table 1).

There is a well-known relationship between predator and prey sizes (Hespenheide 1973, Wilson 1975) that also appears to hold in intraspecific comparisons (Schoener 1967, Roughgarden 1974). It is therefore surprising that a three-fold difference in MWSM between Chilean and Spanish Barn Owls is not related to any significant difference in mean body weight of both owl populations (Table 3). This may be related to the similar configuration of the set of sympatric owl species in the two regions. Both assemblages are equivalent in species number and show a similar patterning in the relative distribution of body sizes (weight and wing length). The Barn Owl is the only species occurring in both areas, although two other congeneric species pairs exist. For the Spanish assemblage, detailed food data for all species reveal a clearcut interspecific segregation in type and size of prey associated with a close relationship between owl and prey sizes (Herrera and Hiraldo 1976). Marti (1969, 1974) described a similar pattern for the owl species in a grassland habitat.

No equivalent information is available for the Chilean assemblage as a whole, but the analysis of the subset formed by the three most common species (Barn Owl; Burrowing Owl, *Athene cunicularia*; Great Horned Owl, *Bubo virginianus*; see Jaksić et al. 1977) suggests a similar situation. These species exhibit clear differences in mean prey size, corresponding closely to differences in owl size. Herrera and Hiraldo (1976) proposed that the owl assemblages in mediterranean habitats exhibit a well-defined resource partitioning, based on prey type and size. If this pattern has evolved in response to interspecific competition, there should be strong selection against deviations in body size from the "species' norm" due to the competitive pressures of adjacent owl species. This should be especially important for a species like the Barn Owl, which is situated in the middle of the size range (Table 3) and is presumably subjected to strong diffuse competition from neighbors.

Because responses of individual owl species to changes in environmental conditions depend upon community relationships, further studies on Chilean owl species are needed for interregional comparisons of community patterns. Such comparisons also require more detailed knowledge of prey populations and of factors responsible for the marked difference in the prey-weight distribution between central Chile and southern Spain.

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LITERATURE CITED

VAN DER BRINK, F. H. 1968. A field guide to the mammals of Britain and Europe. Boston, Houghton Mifflin Co.

DI CASTRI, F., & H. A. MOONEY (Eds.). 1973. Mediterranean type ecosystems: origin and structure. New York, Springer-Verlag.

CLARK, R. J., D. G. SMITH, & L. H. KELSO. 1978. Working bibliography of owls of the world. Washington, D. C., Natl. Wildl. Fed., Sci. Tech. Publ. No. 1.

DEMENTIEV, G. P., & N. A. GLADKOV. 1966. Birds of the Soviet Union. Vol. 1. Jerusalem, Israel Program for Sci. Transl.

FULK, G. W. 1976. Owl predation and rodent mortality: a case study. Mammalia 40: 423–427.

HERRERA, C. M. 1973. Régimen alimenticio de *Tyto alba* en España sudoccidental. Ardeola 19: 359–394.

———. 1974. Trophic diversity of the Barn Owl *Tyto alba* in continental western Europe. Ornis Scandinavica 5: 181–191.

———, & F. HIRALDO. 1976. Food-niche and trophic relationships among European owls. Ornis Scandinavica 7: 29–41.

HESPENHEIDE, H. A. 1973. Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4: 213–229.

JAKSIĆ, F. M., & J. L. YÁÑEZ. 1978. Variación anual de la composición comunitaria de micromamíferos en Los Dominicos, Santiago. Noticiario Mensual, Museo Nacional Historia Natural (Chile) 267: 10–11.

———, & ———. 1979. The diet of the Barn Owl and its relation to the availability of prey. Auk 96: 619–621.

———, E. R. FUENTES, & J. L. YÁÑEZ. 1979. Spatial distribution of the Old World rabbit (*Oryctolagus cuniculus*) in central Chile. J. Mammal. 60: 207–209.

———, J. L. YÁÑEZ, R. PERSICO, & J. C. TORRES. 1977. Sobre la partición de recursos por las Strigiformes de Chile central. Anales Museo Historia Natural Valparaíso (Chile) 10: 185–194.

KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pp. 23–63 *in* Behavioural ecology: an evolutionary approach (J. R. Krebs and N. B. Davis, Eds.). Oxford, Blackwell.

MARTI, C. D. 1969. Some comparisons of the feeding ecology of four owls in northcentral Colorado. Southwestern Natur. 14: 163–170.

———. 1974. Feeding ecology of four sympatric owls. Condor 76: 45–61.

PYKE, G. H., H. R. PULLIAM, & E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137–154.

REISE, D. 1970. Algunos datos sobre la alimentación de la lechuza blanca (*Tyto alba*). Boletín Ornitológico (Chile) 2: 7.

ROUGHGARDEN, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. Amer. Natur. 108: 429–442.

SCHAMBERGER, M. L., & G. W. FULK. 1974. Mamíferos del Parque Nacional Fray Jorge. Idesia (Chile) 3: 167–179.

SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science 155: 474–477.

———. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2: 369–404.

SCHLATTER, R. P., B. TORO, J. L. YÁÑEZ, & F. M. JAKSIĆ. 1980. Prey of the White-tailed Kite in central Chile and its relation to the hunting habitat. Auk 97: 186–190.

———, J. L. YÁÑEZ, H. NÚÑEZ, & F. M. JAKSIĆ. 1980. The diet of the Burrowing Owl in central Chile and its relation to prey size. Auk 97: 616–619.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman & Co.

THROWER, N. J. W., & D. E. BRADBURY (Eds.). 1977. Chile-California mediterranean scrub atlas: a comparative analysis. Stroudsburg, Pennsylvania, Dowden, Hutchinson, & Ross.

UTTENDÖRFER, O. 1939. Die Ernährung der deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur. Berlin, Neudamm.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. Amer. Natur. 109: 769–784.