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FOOD HABITS OF THE GREAT HORNED OWL IN NORTHWESTERN ARGENTINE PATAGONIA: THE ROLE OF INTRODUCED LAGOMORPHS

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ABSTRACT.—Pellets of adult and nestling Great Horned Owls (*Bubo virginianus*) were collected at 12 owl territories near Junín de los Andes (Neuquén, Argentine Patagonia) during the breeding seasons of 1991–92 and 1994–95. Mammals represented 69% of the total prey items (N = 1324) identified and *Reithrodon auritus* (16%), *Lepus europaeus* (12%) and *Ctenomys haigi* (12%) were the most common species. Arthropods accounted for 27% of the total prey by numbers. The two main prey items by biomass were the introduced lagomorphs *L. europaeus* and *Oryctolagus cuniculus* (55%) and those prey that we identified were mainly young that weighed <1000 g. There were no major variations in the diets of owls between mountain and plains areas, but the diversity of small mammals taken was higher in mountain areas. In plains areas, analysis of variation between the first and second halves of the brood-rearing period showed that rodents increased in the diet near the time of fledging. We felt that the low frequency of lagomorphs in the diet of Patagonian Great Horned Owls in comparison with horned owls at similar latitudes in the northern hemisphere may have been due to the fact that Patagonian horned owls weighed 30–40% less and were constrained in the predatory habits by the large size of adult lagomorphs. Large rodents and young lagomorphs may be more optimal prey for Great Horned Owls in Patagonia.

KEY WORDS: *Great Horned Owl; Bubo virginianus; food habits; lagomorphs; Patagonia.*

Dieta de *Bubo virginianus* en el noroeste de la Patagonia argentina: el papel de los lagomorfos introducidos

RESUMEN.—Se colectaron 491 egagrópilas de ñacurutú (*Bubo virginianus*) en el área de Junín de los Andes (Neuquén, Patagonia argentina) durante las estaciones reproductivas de 1991–1992 y 1994–1995. Los mamíferos fueron el 69% del total de presas (n=1324) dominando *Reithrodon auritus* (16%), *Lepus europaeus* (12%) y *Ctenomys haigi* (12%). Los artropodos representaron el 27% de las presas. La principal contribución en biomasa provino de los lagomorfos introducidos *L. europaeus* y *Oryctolagus cuniculus* (55%). Los lagomorfos predados fueron juveniles de menos de 1000 g de peso. No se detectaron variaciones en la dieta entre localidades de montaña y de llanura pero la diversidad de roedores en la dieta fue mayor en la montaña. En una localidad de llanura, el analisis de la variación de la dieta entre dos partes del periodo de desarrollo de pollos en el nido reveló un incremento en los roedores hacia la época de vuelo de los pollos. La baja frequencia de lagomorfos en la dieta de los búhos patagónicos respecto a conespecíficos de latitudes norteñas equivalentes podría ser debida al pequeño tamaño del predador en comparación con el del lagomorfo adulto. Los roedores de gran tamaño y los jóvenes lagomorfos pueden ser las presas más óptimas.

[Traducción Autores]

The Great Horned Owl (*Bubo virginianus*) is distributed throughout North and South America in all biomes except the tundra (Burton 1973). Although its food habits are well known in North America, in temperate South America reports are scarce. Data are available from three localities of the Mediterranean and arid biomes of Chile

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(Yáñez et al. 1978, Jaksić and Yáñez 1980, Jaksić et al. 1986), and in one of the Argentine Pampas (Jaksić 1983). In addition, Yáñez et al. (1978), Jaksić et al. (1986) and Iriarte et al. (1990) have compared the food habits of the species in two different areas from the Chilean Patagonia.

Two Old World lagomorph species, the European hare (*Lepus europaeus*) and the rabbit (*Oryctolagus cuniculus*), have been introduced recently in Patagonia (Housse 1953, Grigera and Rapoport 1983). The Great Horned Owl preys heavily on lagomorphs in many regions of North America (see Donázar et al. 1989). In central Chile, however, despite their high densities, hares and rabbits have shown a low incidence in the owl's diet. This is perhaps due to a failure to adapt to the capture of novel prey (Jaksić and Soriguer 1981), or to an "escape in size" of prey with respect to the owl's size or to the high availability of small mammals as alternative prey (Jaksić 1986).

In this paper, we describe the diet of the Great Horned Owl during the breeding season in northwestern Argentine Patagonia. We examine geographical and seasonal variations and discuss which factors may determine the frequencies of the two introduced lagomorphs in the owl's diet.

METHODS

The study area was located within a radius of 70 km around the city of Junín de los Andes, province of Neuquén, Argentina (70°30′–71°30′W; 39°30′–40°20′S). The area is in the Precordilleran region (Pearson and Pearson 1982) and has a steep transition from lowland plains to the Andean piedmont mountains, the city of Junín being in the transition zone between the two areas. Mountains occupy the northwestern part of the study area, with peaks reaching 1600 m. Plains (600 m elevation) are in the southeastern part of the study area and are dissected by steep valleys. The weather is cold and dry with a pronounced gradient of rainfall from the mountains (800 mm mean annual precipitation) to the plains (300 mm). The area is in the Patagonian phytogeographic province, Western District (Cabrera 1976). The vegetation is typically mixed grass and shrubs. Dominant herbaceous species are *Mullinum spinosum*, *Senecio* spp., *Stipa* spp. and *Poa* spp. The most common shrubs are *Chacaya trinervis*, *Berberis darwinii* and *Schinus molle*. In valley bottoms and topographic depressions, there are marsh zones, called "mallines," with dense herbaceous vegetation where dominant plant species are *Cortadiera araucana*, *Juncus* spp. and *Carex* spp. Woody species such as *Maytenus boaria* and *Salix humboldtiana* are frequent in valleys and near mallines, particularly in the mountain area.

We collected Great Horned Owl pellets during the owl's breeding season from October–December 1991–92, and from October–January 1994–95. We collected samples at 12 breeding sites. Only fresh pellets were sampled and we discarded those that might have been regurgitated prior to or after the breeding season. At one of the plains nesting sites, we made two visits in late November and early January which corresponded with the first and second half of the nestling period.

Prey remains were identified using skull taxonomic keys (for small mammals, Pearson 1986) and voucher specimens (lagomorphs, birds, reptiles and arthropods) collected in the study area and in museum collections. Weight of lagomorphs appearing in pellets was estimated from comparisons to skeletons of rabbits and hares of known weight collected in the study area. Individuals were ascribed to one of three classes according to body mass: <300 g, 300–1000 g, and >1000 g.

To describe the diet of the Great Horned Owls in our study, we used the parameters proposed by Jaksić et al. (1986): (1) geometric mean of the prey based on biomass values of small mammals obtained from Pearson (1984) and Redford and Eisenberg (1992); lagomorphs from comparisons with skeleton collections, and birds, reptiles, amphibians and arthropods from voucher specimens. (2) Diet breadth calculated with Levins' (1968) index: $B_{obs} = 1/pi^2$), where pi is the relative frequency of each prey taxon; this index varies from 1-n. (3) Standardized diet breadth calculated following Colwell and Futuyma (1971): $B_{sta} = (B_{obs} - B_{min})/(B_{max} - B_{min})$ where $B_{min} = 1$ and $B_{max} = n$. Its value ranges from 0–1 and permits one to establish comparisons between samples with different numbers of prey categories.

Partitionings of Chi-square contingency tables were made after Siegel and Castellan (1988).

RESULTS

We identified 1324 prey items in 491 pellets (Table 1). Mammals comprised the majority of prey (69%); the species most eaten were *Reithrodon auritus* (16%), *Lepus europaeus* (12%) and *Ctenomys haigi* (12%). Arthropods were next in numerical frequency, with Coleopterans (21%) and Scorpionidans (5%) the most common. Birds (3%), reptiles (1%) and amphibians (0.4%) were poorly represented. Based on biomass, the main prey was the European hare (46%), followed by *C. haigi* (14%), *R. auritus* (11%) and *O. cuniculus* (9%). The biomass of reptiles, amphibians and arthropods was negligible (<1%).

Rabbit remains occurred less frequently in pellets than did European hares. Both rabbits and hares were available as prey at four nesting areas. In three of these areas, hares occurred more frequently than rabbits in the diets (9.7 vs. 2.3%, $N = 308$; 15.1 vs. 2.6%, $N = 544$; 27.8 vs. 9.7%, $N = 72$). In the fourth nesting area, rabbits occurred over 3 times more frequently in the diet (12.5 vs. 37.5%, $N = 40$). The 38 European hares we identified most were small- and medium-sized individuals; 30 (78.9%) were <300 g and 8 (21.0%) 300–

Table 1. Prey consumed by Great Horned Owls in Junín de los Andes region (Neuquén, Argentinian Patagonia). We show data for two different physiographic areas: mountain and plains. Percent composition is shown for numeric frequencies (%n) and biomass (%b).

Prey	Weight (g)[a]	Mountain n	Mountain %n	Plains n	Plains %n	Total n	Total %n	Total %b
MAMMALIA		643	68.7	261	68.7	904	68.7	91.4
Ctenomys haigi	164	104	10.3	50	15.7	154	11.6	13.7
Galea musteloides	226	—	—	2	0.6	2	0.1	0.3
Microcavia australis	286	—	—	4	1.2	4	0.3	0.7
Galea or *Microcavia*	256	—	—	19	6.0	19	1.4	3.0
Akodon sp.	29	12	1.2	54	16.9	66	5.0	1.2
Auliscomys micropus	73	21	2.1	—	—	21	1.6	0.9
Chelemys macronix	72	5	0.5	—	—	5	0.4	0.2
Eligmodontia typus	21	18	1.8	15	4.7	33	2.5	0.4
Euneomys sp.	85	15	1.5	—	—	15	1.1	0.8
Geoxus valdivianus	26	6	0.6	—	—	6	0.4	0.1
Oryzomys longicaudatus	33	13	1.3	2	0.6	15	1.1	0.3
Phyllotis darwini	58	25	2.5	12	3.8	37	2.8	1.3
Reithrodon auritus	82	185	18.4	32	10.0	217	16.4	10.9
Calomys musculinus	18	1	1.0	—	—	1	0.1	—
Rattus norvegicus	250	2	2.0	—	—	2	0.1	0.3
Unidentified rodents	30	77	7.7	30	9.4	107	8.0	2.0
Marmosa pusilla	60	1	1.0	1	0.3	2	0.1	0.1
Oryctolagus cuniculus	334*	36	3.6	10	3.1	46	3.5	9.4
Lepus europaeus	475*	127	12.6	30	9.4	157	11.9	45.8
AVES		28	2.8	5	1.6	33	2.5	7.7
Anas sp.	800	5	0.5	—	—	5	1.6	2.5
Milvago chimango	260	3	0.3	—	—	3	0.2	2.4
Falco sparverius	130	2	0.2	1	0.3	3	0.2	0.2
Callipepla californica	205	6	0.6	—	—	6	0.4	0.7
Vanellus chilensis	298	7	0.7	—	—	7	0.5	1.3
Zenaida auriculata	129	1	1.0	1	0.3	2	0.1	0.2
Caprimulgus longirostris	80	—	—	1	0.3	1	0.1	—
Sturnella loyca	111	1	1.0	—	—	1	0.1	0.1
Unidentified Passeriform	70	2	0.2	2	0.6	4	0.3	0.2
Unidentified bird	80	1	1.0	—	—	1	0.1	0.1
REPTILIA		4	0.4	11	3.4	15	1.1	0.4
Iguanidae	19	—	—	2	0.6	2	0.1	—
Serpentes	200	2	0.2	—	—	2	0.1	0.2
Unidentified reptile	20	2	0.2	9	2.8	11	0.8	0.1
AMPHIBIA		5	0.5	—	—	5	0.4	—
Anura	10	5	0.5	—	—	5	0.4	—
ARTHROPODA		278	27.7	84	26.3	362	27.3	0.5
Coleoptera	2	240	23.9	44	13.7	284	21.4	0.3
Araneae	2	—	—	1	0.3	1	0.1	—
Solifugae	2	2	0.2	1	0.3	3	0.2	—
Scorpionida	4	34	3.4	38	11.9	72	5.4	0.2
Crustacea	7	2	0.2	—	—	2	0.1	—
Total prey		1005		319		1324		
Geom. mean weight of prey		36.3		32.2		36.5		
Bobs		7.22		10.65		8.67		
Bsta		0.16		0.26		0.20		

[a] Weights were means calculated from numeric frequencies of each biomass category (see methods).

Table 2. Geographic (mountain and plains) and seasonal variations in prey frequencies by number in the diet of Patagonian Great Horned Owls. Seasonal variation was examined in a plains locality: November and December samples correspond to the first and second half of the nestling period, respectively. For statistical treatments, birds, reptiles and amphibians were pooled in a single category.

	GEOGRAPHIC		SEASONAL	
PREY	MOUNT.	PLAINS	NOV.	DEC.
Rodents	52.4	55.9	46.7	61.7
Lagomorphs	16.2	12.5	14.9	10.5
Birds	2.8	1.6	1.9	1.5
Reptiles	0.4	3.4	1.9	4.5
Amphibians	0.5	—	—	—
Arthropods	27.7	26.3	34.6	21.9
Chi-square	3.953		8.892	
df	3		3	
P	0.267		0.031	

1000 g. We also caught and weighed 136 European hares. Of these, 61 (44.9%) were <300 g, 74 (54.4%) 300–1000 g and 1 (0.7%) >1000 g.

The diet of Great Horned Owls did not show clear differences between mountain and plains areas (Table 2). The geometric mean of prey biomass was similar between the two areas (36.3 g in mountains and 32.2 g in plains) but diet breadth indices were higher in plains (B_{obs}: 7.22 vs. 10.65, B_{sta}: 0.16 vs. 0.26). More rodent species occurred in the diet of horned owls in mountainous areas than on the plains (12 vs. 8 species). Six species were taken exclusively in mountains: *Auliscomys micropus, Chelemys macronyx, Euneomys* sp, *Geoxus valdivianus, Calomys musculinus* and *Rattus norvegicus,* whereas only two were exclusive to the plains: *Galea musteloides* and *Microcavia australis.*

There was a significant seasonal variation in the diet at one of the plains nesting areas (Table 2). Partitioning of the degrees of freedom of the Chi-square table revealed that birds plus reptiles, in comparison to lagomorphs, and then to arthropods, did not differ in their frequencies between the first ($P > 0.20$) and second part ($P > 0.50$) of the nestling period with rodents being consumed significantly more in the last part of the breeding period than in early stages ($\chi^2 = 6.360$, df = 1, $P < 0.02$). Between the first and second halves of the nestling period, the geometric mean of prey biomass nearly doubled from 25.0 to 49.3 g and the niche breadth increased (B_{obs} from 8.72 to 9.85, B_{sta} from 0.21 to 0.24).

DISCUSSION

Our results indicate that, in Patagonia, as elsewhere, the Great Horned Owl is a generalist predator taking prey ranging from invertebrates to lagomorphs. We found its most common prey in Patagonia to be small- and medium-sized mammals such as rodents and young lagomorphs. Rodents (14 species) made up 53% of the diet by numbers and two species, *Ctenomys haigi* and *Reithrodon auritus,* were the dominant prey. In this same area, Barn Owls (*Tyto alba*) have been also been reported to preferentially capture *R. auritus,* but they also take the smaller *Akodon* sp. and *Eligmodontia typus* in numbers that closely follow their availability (Pearson 1986, Travaini et al. 1997). Therefore, it appears that the larger sized Great Horned Owl selects larger rodent species with relatively high biomass, relative to the Barn Owl (see also Jaksić and Yáñez 1980). The Great Horned Owl also hunts from perches (Rudolph 1978) and thus may benefit by concentrating its foraging activity in predictable places with high prey densities such as areas that support colonies of *C. haigi. Ctenomys* species spend most of their life underground but they probably become vulnerable to owl predation when they forage at night in the vicinity of burrow entrances (Redford and Eisenberg 1992).

The observed differences in rodent diversity in the diet of Great Horned Owls between mountains and plains (12 vs. 8 species) may reflect the composition of local rodent assemblages which are more diverse in the humid, open areas of the Andean precordillera (Pearson and Pearson 1982). This difference may also be related to the introduction of European lagomorphs which has undoubtedly reduced the reliance of horned owls on rodents in the plains areas of Patagonia.

Lagomorphs represent 15% by numbers in the diet of Great Horned Owls in Argentine Patagonia whereas in Chilean Patagonia the numeric frequencies vary during spring and summer from 0.6 to 5.3% (Jaksić et al. 1986). In both areas, the occurrence of lagomorphs in the diet is lower than in similar latitudes in the Northern Hemisphere where lagomorphs reach 29.3% in temperate forests, 24.2% in grasslands, 19.0% in Mediterranean scrubland and 15.7% in mountain areas (see Donázar et al. 1989). The relatively low presence of lagomorphs in the diet of Patagonian Great

Horned Owls is unlikely due to "novel prey rejection" (Jaksić and Soriguer 1981), because European hares have been in this area since 1900 (Grigera and Rapoport 1983) and they are now very abundant reaching spring-summer densities of 2000 individuals/km^2 (Novaro et al. 1992). Rabbits appeared only 5-yr ago in this area of Patagonia but they have already reached densities greater than in Europe (Howard and Amaya 1975).

More likely, the low incidence of lagomorphs in the diet of Patagonian horned owls is related to their ability to "escape by size" (Jaksić 1986). That is, lagomorphs (adult animals) are much too large to be captured by this relatively small form of Great Horned Owl. Two freshly dead Great Horned Owls in our study area weighed 820 and 910 g. This was 30–40% less than the body mass of horned owls living at similar latitudes in North America (1543 g for *B. v. virginianus* and 1354 g for *B. v. occidentalis,* Earhart and Johnson 1970). Adult European hares in the study area have a mean body mass of 3250 g, reaching up to 4600 g whereas adult rabbit body mass is around 1700 g (Amaya 1979). As a result, Great Horned Owls are only able to capture European hares when young. Hares are certainly available, as evidenced by the fact that the Grey Eagle-buzzard (*Geranoaetus melanoleucus*), a larger raptor living in the study area, includes up to 76% of hares in its diet and even displays a functional response by capturing more hares during the summer probably as a consequence of their higher availability and of the eagle increase in breeding requirements (Hiraldo et al. 1995, Pávez et al. 1992).

Small Patagonian Great Horned Owls may actually obtain a higher energetic yield from rodents than larger Great Horned Owls in North America (Jaksić 1986). Because prey species such as *C. haigi* concentrate in predictable places, the energetic expenditure of small owls for hunting rodents may be very low in comparison to that of solitary hares. Higher capture rates of locally common medium-sized rodent species have also been reported for other *Bubo* species in European Mediterranean ecosystems, even when the rabbit is abundant (Donázar 1987).

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