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ORIGINAL ARTICLE

Diet of the Red-backed Hawk (*Buteo polyosoma*) in two environmentally contrasting areas of Patagonia

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We studied the Red-backed Hawk (*Buteo polyosoma*) diet by pellet analysis in two areas, the Monumento Natural Bosques Petrificados (MNBP) and Junín de los Andes, located in southern and northwestern Argentinean Patagonia respectively. These areas have different values of primary production mainly due to the differences in mean annual precipitation, being higher in Junín de los Andes. Diets were dominated by mammals in both areas (68.3% and 61% of occurrences). Rodents represented the greatest proportion (66.5%) of prey numbers in MNBP. They represented 92.6% of the biomass. Arthropods were also consumed with a relatively high occurrence (21.4%). In Junín de los Andes, rodents were an important prey (57.1%) but represented only 29.6% of the consumed biomass. In contrast, the introduced European hare (*Lepus europaeus*) was not frequently consumed (13.5%) but comprised 59.3% of prey biomass. Reptiles were a frequent item, consumed at 25.2% of total prey. The diet of the Red-backed Hawk was significantly different between MNBP and Junín de los Andes. The wider food niche breadth of the Red-backed Hawk in Junín de los Andes was likely attributable to the more even distribution of prey categories. Additionally, a functional response toward European hare consumption was observed, with a higher consumption of this prey at Junín de los Andes.

Estudiamos la dieta del Aguilucho común (*Buteo polyosoma*) por medio del análisis de egagrópilas, en dos áreas: el Monumento Natural Bosques Petrificados (MNBP) y Junín de los Andes, situadas respectivamente en el sur y noroeste de la Patagonia Argentina. La productividad primaria es diferente en ambas áreas, debido principalmente a la cantidad de precipitaciones, que son mayores en Junín de los Andes. Los mamíferos fueron las presas más importantes en la dieta del Aguilucho en ambas áreas (68.3% y 61.0% de ocurrencias). La proporción de roedores en el MNBP fue alta (66.5%), representando el 92.6% de la biomasa total consumida. Otro ítem importante fueron los artrópodos con una ocurrencia del 21.34%. En Junín de los Andes, los roedores fueron también presas importantes en la dieta del Aguilucho común (57.1%), pero representaron solamente 29.6% de la biomasa total consumida. Por el contrario, la liebre europea (*Lepus europaeus*), una presa introducida, fue consumida con una frecuencia menor (13.5%) pero constituyó el 59.3% de la biomasa total. Los reptiles fueron frecuentemente consumidos (25.2%). En concordancia, la dieta del Aguilucho común fue significativamente diferente entre el MNBP y Junín de los Andes. La mayor amplitud del nicho trófico del Aguilucho común en Junín de los Andes podría ser atribuida a la mayor equidad en la distribución de las categorías presa. Adicionalmente, se observó una respuesta funcional hacia el consumo de liebre europea, siendo mayor en Junín de los Andes.

Keywords: *Buteo polyosoma*; diet; functional response; European hare; Argentinean Patagonia

Introduction

The Red-backed Hawk (*Buteo polyosoma*) is a medium sized raptor widely distributed in South America from the central Andes of Colombia to the Cape Horn Archipelago in Chile (Brown & Amadon 1968; Del Hoyo et al. 1994). Despite its wide distribution and commonness, general information on its biology is scarce (Baladrón et al. 2006, but see Jiménez 1995). Red-backed Hawks have a wide prey spectrum, including mammals (mostly rodents), birds, reptiles, amphibians, and invertebrates (Schlatter et al. 1980; Del Hoyo et al. 1994; Jiménez 1995; Figueroa et al. 2003; Baladrón et al. 2006), and occasionally carrion (Brown & Amadon 1968; Woods 1975; Fuentes et al. 1993). The hawk's diet progressively diversifies southwards, being mainly composed of birds, lagomorphs, reptiles and amphibians (Baladrón et al. 2006). At the southern end of its range, the diet is composed exclusively of small mammals (Figueroa et al. 2003; Baladrón et al. 2006). Based on the analysis of

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78 pellets collected in four sampling sites in northwestern Argentinean Patagonia, Monserrat et al. (2005) reported that the Red-backed Hawk is a generalist predator. In contrast, Baladrón et al. (2006) described the Red-backed Hawks in the southeastern coast of Buenos Aires Province as rodent specialists, based on the analysis of 80 pellets.

We studied the Red-backed Hawk's diet in two different areas in Argentinean Patagonia: the Monumento Natural Bosques Petrificados, a protected area located in southern Patagonia and Junín de los Andes, located in northwestern Patagonia. Both areas differ in their mean annual rainfall and plant productivity, although they are quite similar in habitat structure, with the latter being more rainy and productive. Our aims are (1) to quantitatively describe the diet of the Red-backed Hawk in southern continental Patagonia, including a comparison of the diet of this species between both areas. We expect a more diversified diet in northwestern Patagonia and a greater abundance of small mammals in the southern locality. We also intended (2) to determine the importance level of the introduced European hare (*Lepus europaeus*) in the hawk's diet. Previous studies conducted in Patagonia showed that it is a profitable prey for the raptor assemblage (Travaini et al. 1996) favoring functional responses as a consequence of its high availability (Hiraldo et al. 1995).

Materials and methods

Study areas

We conducted our study in two areas in Argentinean Patagonia. One of them, the Monumento Natural Bosques Petrificados National Park (MNBP, 47°40′ S; 67°60′ W), is a protected area located in Santa Cruz province, southern Patagonia (Figure 1) that corresponds to the phytogeographical Patagonian province, Central District (León et al. 1998). It is a shrub-steppe, locally known as "erial", whose vegetal cover does not exceed the 50%. Dominant grass species in MNBP are *Stipa* spp., *Festuca pallescens*, *Poa dusenii* and *Carex argentina*. Common shrubs are *Junellia tridens* (Verbenaceae) and *Nassauvia glomerulos* (Compositae). In the ravines, vegetation is dominated by *Anartrophyllum rigidum* (Leguminosae), *Schinus polygamus* (Anacardiaceae) and *Berberis heterophylla* (Berberidaceae). The weather is dry and cold, with frequent frosts. Mean annual temperatures are about 10°C, with highest temperatures during summer (30°C for January and February) and lowest during autumn and winter (–10°C from May to July). Annual rainfall ranges between 100 and 300 mm. The other area, located in Neuquén province, northwestern Patagonia, included the surroundings of Junín de los Andes city (39°57′ S; 71°05′ W, Figure 1), and corresponds to the Patagonian phytogeographical province, occidental district (León et al. 1998). The topography is similar to the MNBP as is the vegetation structure, although vegetal cover exceeds the 50%. Dominant grass species are *Stipa* spp., and *Poa* spp., while common shrubs are *Mulinum spinosum* (Apiaceae), *Chacaya trinervis* (Rhamnaceae), *Berberis darwinii* (Berberidaceae), *Senecio* spp. (Compositae) and *Schinus molle* (Anacardiaceae). The annual rainfall ranges between 300 and 700 mm, and mean annual temperatures are about 11°C. In both areas, the most important weather feature is strong cold winds that can reach speeds of up to 120 km h^{-1}. During spring, they blow from the Andean range, in an easterly direction, towards the Patagonian steppe. Plant primary production is contrasting between both sites, mainly due to the differences in mean annual precipitation (Paruelo et al. 1998), being higher in Junín de los Andes.

Pellet collection, prey identification and diet analysis

From February 1999 to September 2008, we collected pellets in MNBP at three sites: Laguna El Vasco (S1), El Cuadro (S2) and Cerro Horqueta (S3) (Figure 1). In Neuquén province we collected pellets from November 1992 to April 1993, at seven sampling sites located within a radius of 60–70 km around the city of Junín de los Andes: Quilquihue (S4), Puesto Álamo and Quemquemtreu (S5), Cerrito Piñón (S6), La Rinconada (S7), Catan Lil (S8), Mendaña (S9) and the Collon-cura river valley (S10). Pellets were collected near known hawk perches or nests and analyzed using standard techniques (Marti et al. 2007). They were hydrated and broken apart by hand for prey remains identification. Smalls mammals were identified to species on the basis of skulls, dentaries, hairs and claws, using reference collections and keys (Chehébar & Martin 1989; Pearson 1995). We discriminated between juvenile and adult individuals of European hares (*Lepus europaeus*) and tuco-tucos (*Ctenomys* sp.) respectively, by the examination of their tooth wear patterns and comparing them with a reference collection. Birds and reptiles were identified to species when possible by comparing skull and mandible remains and feathers with a reference collection. Arthropods were identified to the finest taxonomic level possible, comparing elytra, heads, mandibles, and any other identifiable parts with a reference collection.

Biomass contribution of each prey type (B%) was estimated following the method of Marti et al. (2007): $B\% = 100[(Sp_i\ N_i)/\Sigma\ (Sp_i\ N_i)]$, where Sp_i is the mass of the species i, and N_i is the number of individuals

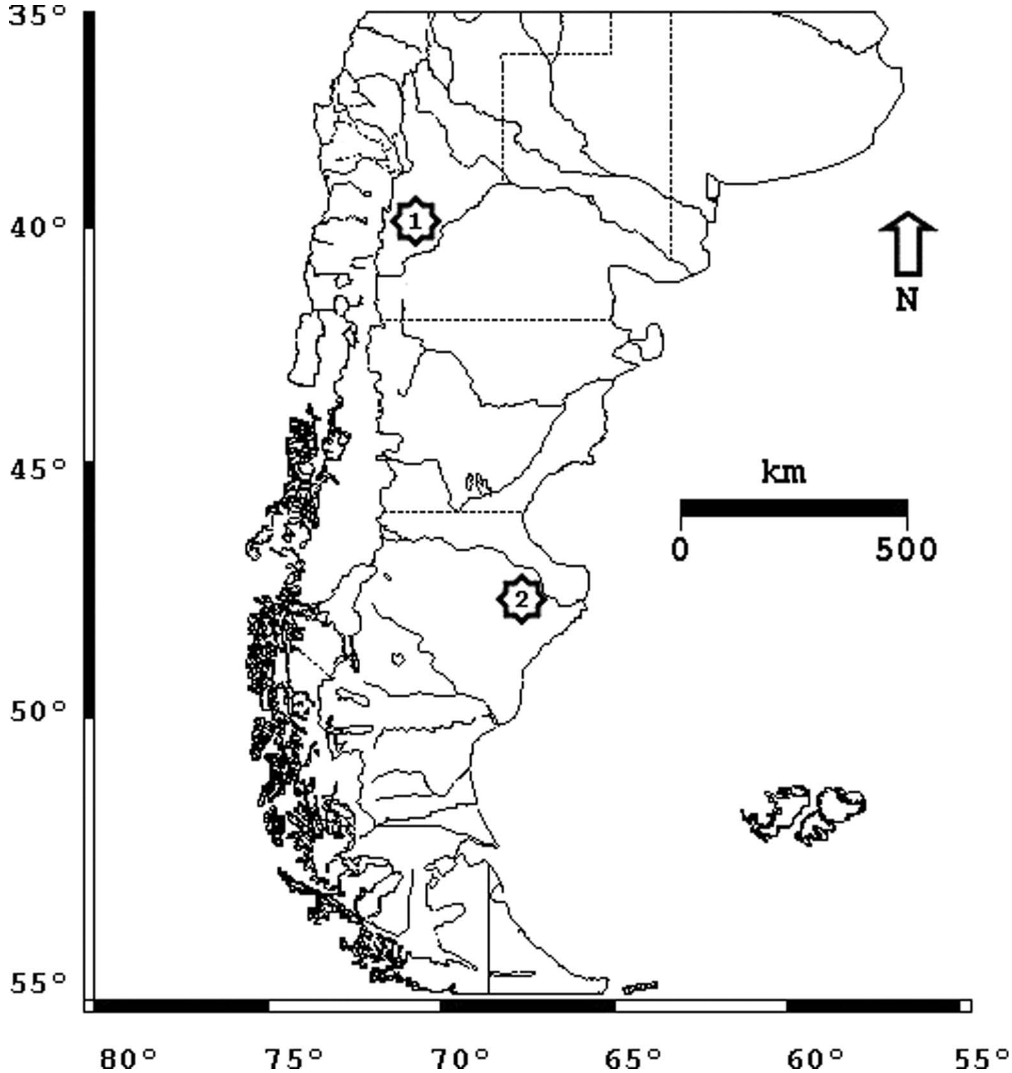

Figure 1. Study areas: (1) Junín de los Andes, Neuquén province, northwestern Patagonia; (2) Monumento Natural Bosques Petrificados, Santa Cruz Province, southern Patagonia, Argentina.

of the species i consumed. Biomass of small mammals and birds was obtained from the literature and our unpublished records. Each specimen found in a pellet was considered to be one complete prey item, except for the European hare, for which we assumed a maximum consumed biomass of 300g per pellet (Trejo et al. 2006). Following Vargas et al. (2007), a biomass of 1 g was assigned to each invertebrate prey item. Diet was expressed as the percentage of total prey items and as consumed biomass by grouping total prey analyzed from the different sampling sites for both study areas.

We then calculated Colwell & Futuyma's (1971) standardized form (B_{sta}) of Levins' index (B) to measure food-niche breadth (Levins 1968), an index of diet diversity:

$$B_{sta} = (B_{obs} - B_{min})/(B_{max} - B_{min}), \quad (1)$$

where B_{obs} is the observed niche breadth, $B_{min} = 1$ is the minimum niche breadth, and B_{max} is the maximum possible niche breadth (the number of taxa taken). B_{obs} is $= 1/\Sigma\ p_i^2$, where p_i is the relative occurrence of prey taxon i in the diet. The B_{sta}, which ranges from 0 to 1 (i.e. from narrow to broad food niche), allows comparison of diets with different numbers of prey categories. We measured food niche breadth by grouping all different prey items into five categories: rodents, lagomorphs, birds, reptiles and arthropods. To evaluate differences in the occurrences of the prey categories between MNBP and Junín de los Andes we used *G*-test (Sokal & Rohlf 1981). This test is the preferred statistic when categories are not derived from the data themselves, i.e. numbers versus proportions of prey (Dytham 2000). As we were also interested in the determination of similarities among diets of the species in the different sites of both localities, MNBP and Junín de los Andes, we used cluster analysis (complete linkage technique, Euclidean distance, McGarigal et al. 2000). For this purpose diets were expressed in frequencies of food categories. Principal component analysis (PCA), calculated on a correlation matrix, was used to assess which food categories generated the pattern found in cluster analysis (Digby and Kempton 1994; Manly 1994). Density value of European hares in MNBP was obtained from a study performed in the MNBP (A. Travaini, M. Santillan, S. Zapata, unpublished data) based on the line transect methodology (Bibby et al. 1992).

Results

We collected a total of 268 and 282 Red-backed Hawk pellets at MNBP and Junín de los Andes, respectively. Diet was described based on 432 and 520 prey items from these localities, respectively.

The diet of the Red-backed Hawk in MNBP consisted mainly of mammals, with a frequency of 68.3% and representing 97.1% of the total biomass consumed. Birds (at least seven species, 4.8% frequency and 1.9% biomass) and reptiles (three species, 5.5% frequency and 0.9% biomass) were rarely consumed (Table 1). Arthropods of three insect and one arachnid orders (Table 1) occurred frequently (21.3%), but contributed little to biomass (0.2%, Table 1). Among mammals, rodents were the most important prey, both in frequency and biomass consumed (66.4% and 92.6% respectively). We identified six rodent species (Table 1), but tuco-tucos (*Ctenomys* sp.) and lesser cavies (*Microcavia australis*) were the most important prey, accounting for 37.9% and 18.5% of frequency respectively, and 42.2% and 47.9% of biomass, respectively (Table 1). These are the heaviest rodent species recorded in the pellets (Table 1). The other mammals, lagomorphs and marsupials were less frequent (Table 1).

In Junín de los Andes, mammals were also the most important prey, with a frequency of 61.0% and representing 88.9% of the consumed biomass (Table 1). Among them, unidentified rodents and *Ctenomys* sp. had a frequency of 44.8% and 2.7% and represented 25.8% and 3.9% of the biomass respectively. European hares, mainly juveniles, contributed to the hawks' diet with the bulk of the biomass (59.3%) (Table 1). Reptiles were also a frequent prey item in the pellets (25.2%) but comprised only 6.5% of the consumed biomass. Arthropods and birds were less important in the hawks' diet (Table 1).

The diet of Red-backed Hawks was significantly different between MNBP and Junín de los Andes (G-test= 154.1; df = 4, $P < 0.001$), mainly due to the higher consumption of lagomorphs and reptiles in Junín de los Andes, and arthropods in MNBP. Niche breadth was higher in Junín de los Andes ($B_{st} = 0.54$) than in MNBP ($B_{st} = 0.26$), pointing out a higher evenness in prey consumption in the first locality.

A cluster analysis comparing similarities among the diets in the two study areas separated them into two principal groups: the three sites from MNBP on one hand and the sites from Junín de los Andes on the other hand, indicating dissimilarities among frequencies of food categories between both localities (Figure 2, Table 2). In Junín de los Andes, sampling sites were grouped into four different groups in the dendrogram, reflecting a more diversified diet in this area (Figure 2, Table 2). Principal components 1 and 2 explained 58.8% and 21.4% respectively of the overall variance of the diet at different sampling sites. The main food categories that contributed to the first axis were rodents and arthropods on the positive side, where the three sites of MNBP and one site of Junín de los Andes were located. On the negative side, lagomorphs, birds and reptiles contributed to this axis, where the remaining sites from Junín de los Andes were located (Figure 3).

Discussion

Food habits of Red-Backed Hawks and comparison between study sites

Red-backed Hawks in MNBP behaved as food specialists, preying mostly on mammals as was reported by Jiménez (1995). Baladrón et al. (2009) described a close trophic association between hawks and tuco-tucos in a coastal locality of Buenos Aires province, because they are profitable prey in terms of the energy available and handling costs. In their work, conducted in winter, young and subadult tuco-tucos were found more frequently in hawks' diet than expected from their field abundances. In contrast, we found that hawks consumed more adult than young tuco-tucos throughout the year, but we did not estimate their relative abundances.

In contrast, in Junín de los Andes, the hawks behaved in a more generalistic way, supporting the findings of Monserrat et al. (2005) in the same area. Accordingly, as we expected, the value of standardized food niche breadth was higher in this locality than in MNBP, although mammals were still the main prey. Nevertheless, we are aware that pellet samples from both MNBP and Junín de los Andes came from very different time periods, as did those studied by Monserrat et al. (2005), facts that could explain such differences. In contrast to our results, high proportions of *Ctenomys* sp. and low proportions of European hare in the hawks' diet were found in Junín de los

Table 1. Frequency and estimated biomass of animal taxa recorded in pellets of Red-backed Hawks at Monumento Natural Bosques Petrificados (Santa Cruz) and Junín de los Andes (Neuquén) Argentinean Patagonia. Body masses were obtained from the literature or from our unpublished data. Abbreviations: ad.: adults, juv: juveniles, n.i.: not identified.

	Monumento Natural Bosques Petrificados ($n = 268$)					Junín de los Andes ($n = 282$)				
	Prey body mass	Frequency		Biomass		Prey body mass	Frequency		Biomass	
Taxa	(g)	N	%	(g)	%	(g)	N	%	(g)	%
Mammals		**295**	**68.29**	**46363.7**	**97.05**		**317**	**60.96**	**31489.06**	**88.86**
Rodents		287	66.44	44213.7	92.55		247	47.5	10489.06	29.60
Cricetidae		42	9.72	1053.87	2.21					
Abrothrix sp.	19.47	9	2.08	175.23	0.37					
Eligmodontia sp.	19.05	26	6.02	495.3	1.04					
Graomys griseoflavus	45.38	3	0.69	136.14	0.28					
Reithrodon auritus	61.8	4	0.93	247.2	0.52					
Caviidae		80	18.52	22888	47.91					
Microcavia australis	286.1	80	18.52	22888	47.91					
Ctenomyidae		164	37.96	20180	42.24					
Ctenomys sp. ad.	125	156	36.11	19500	40.82					
Ctenomys sp. juv.	85	8	1.85	680	1.42					
Ctenomys sp.[a]						98.15	14	2.69	1374.1	3.88
Rodents n.i.[b]	91.82	1	0.23	91.82	0.19	39.12	233	44.81	9114.96	25.72
Lagomorphs		7	1.62	2100	4.40		70	13.46	21000	59.26
Lepus europaeus ad.[c]	300	1	0.23	300	0.63	300	10	1.92	3000	8.47
Lepus europaeus juv.	300	6	1.39	1800	3.77	300	60	11.54	18000	50.79
Marsupials		1	0.23	50	0.10					
Didelphidae n.i.	50	1	0.23	50	0.10					
Birds		**21**	**4.86**	**907.7**	**1.90**		**28**	**1.67**	**1599.5**	**4.51**
Charadriiformes		1	0.23	54.3	0.11					
Thinocoridae										
Thinocorus rumicivorus	54.3	1	0.23	54.3	0.11					
Columbiformes							2	0.38	248.4	0.70
Columbidae										
Zenaida auriculata						124.2	2	0.38	248.4	0.70
Passeriformes		20	4.63	853.4	1.79		26			
Furnariidae										
Furnariidae n.i.	54	1	0.23	54	0.11					
Tyrannidae										
Lessonia rufa						13.4	1	0.19	13.4	0.04
Emberizidae										
Emberizidae n.i.	16.8	1	0.23	16.8	0.04					
Icteridae										
Sturnella loica	79.3	2	0.46	158.6	0.33	79.3	9	1.73	713.7	2.01
Passeriformes n.i.	39	16	3.70	624	1.31	39	16	3.08	624	1.76
Reptiles		**24**	**5.56**	**407.49**	**0.86**	**17.6**	**131**	**25.19**	**2305.6**	**6.51**
Leiosauridae										
Diplolaemus sp.	25.37	3	0.69	76.11	0.16					
Liolaemus sp.	14.87	14	3.24	208.18	0.44					
Reptiles n.i.	17.6	7	1.62	123.2	0.26	17.6	131	25.19	2305.6	6.51
Arthropods	**1**	**92**	**21.30**	**92**	**0.19**	**1**	**44**	**8.46**	**44**	**0.12**
Insects	**1**	**85**	**19.68**	**85**	**0.18**	**1**	**44**	**8.46**	**44**	**0.12**
Orthoptera	1	1	0.23	1	0.00	1	39	7.50	39	0.11
Lepidoptera (Larvae)	1	1	0.23	1	0.00		0			
Homoptera	1	25	5.79	25	0.05		0			
Cicadidae										
Cicadidae n.i.	1	3	0.69	3	0.01					
Phasmatodea										
Phyllidae										
Agathemera crassa	1	22	5.09	22	0.05					

(*Continued*)

Table 1. (Continued).

Taxa	Monumento Natural Bosques Petrificados (n = 268) Prey body mass (g)	Frequency N	Frequency %	Biomass (g)	Biomass %	Junín de los Andes (n = 282) Prey body mass (g)	Frequency N	Frequency %	Biomass (g)	Biomass %
Coleoptera	1	58	13.43	58	0.11	1	5	0.96	5	0.01
Scarabaeidae	1	1	0.23	1	0.00					
Carabidae										
Cnemalobus sp.	1	1	0.23	1	0.00					
Curculionidae										
Curculionidae n.i.	1	21	4.86	21	0.04					
Tenebrionidae										
Epidonota sp.	1	1	0.23	1	0.00					
Nyctelia sp.	1	15	3.47	15	0.03					
Tenebrionidae n.i.	1	9	2.08	9	0.02					
Coleoptera n.i.	1	10	2.31	10	0.02					
Arachnids	**1**	**7**	**1.62**	**7**	**0.01**		**0**			
Bothriuridae n.i.	1	7	1.62	7	0.01					
Total prey items		**432**	**100**	**47770.9**	**100**		**520**	**100**	**35438.16**	**100**

[a] Body mass obtained from Monserrat et al. (2005).
[b] Body mass estimated as the mean weight of rodents known to occur in Red-backed Hawks diet in the area.
[c] We assumed a maximum consumed biomass of 300 g per pellet for adults and juveniles European hares (Trejo et al. 2006).

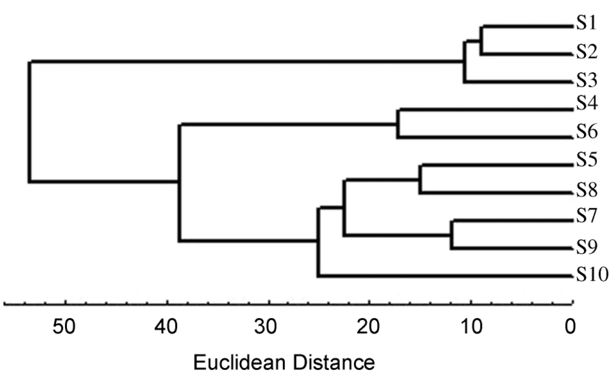

Figure 2. Dendrogram showing similarities (%) among diets (expressed in frequencies of food categories) of the Red-backed Hawk in the different sampling sites of the two study areas, Junín de los Andes (S4 to S10) and Monumento Natural Bosques Petrificados (S1 to S3). For names of the sites see Methods.

Andes (Monserrat et al. 2005) for a period of 10 years subsequent to our study. Both in MNBP and in Junín de los Andes, reptiles and birds were always secondary prey, while invertebrates were seldom consumed as was observed by Fuentes et al. (1993) and Figueroa et al. (2003) in Chile.

Importance level of the introduced European hare

The finding that almost 60% of the biomass consumed by Red-backed Hawks came from European hares in Junín de los Andes shows their ability to switch from native to introduced species, depending on their relative availability, a behavior already described by Pavez et al. (1992) for Black-chested Eagles (*Geranoaetus melanoleucus*) in Central Chile where they markedly shifted their diets from native rodents to European rabbits (*Oryctolagus cuniculus*). Likewise, Monserrat et al. (2005) reported a significant functional response of these eagles to European hares in Junín de los Andes, although they did not detect a functional response of the Red-backed Hawk toward this introduced prey. But, as they stated, this may have been due to their small sample size. Another factor affecting the lack of functional response could be the similar hare abundance among their sampling sites. Contrary evidence arises from our data: the Red-backed Hawk consumed one order of magnitude more European hares where it was more abundant (i.e. Junín de los Andes, with hare density between 0.12 and 0.8 hares ha^{-1} (Monserrat et al. 2005) versus 0.017 hares ha^{-1} in the MNBP).

The majority of hares taken by the hawks were juveniles. Similarly, in central Chile, the Red-backed Hawks took mostly juvenile rabbits, probably because they were unable to kill or handle prey as large as adult rabbits or hares which can weigh over 3 kg (Schlatter et al. 1980). The hawk's prey capture behavior was described as struggling and killing the prey by squeezing it with its talons (Baladrón et al. 2006), thus the size and strength of the talons impose a limit to the size

Table 2. Frequency (in %) of prey taxa recorded in pellets of Red-backed Hawks from different sampling sites from Monumento Natural Bosques Petrificados and Junín de los Andes. n = number of pellets analyzed in each sampling site.

	Monumento Natural Bosques Petrificados			Junín de los Andes						
	S1 El Vasco	S2 El Cuadro	S3 Cerro Horqueta	S4 Quilquihue	S5 Puesto Álamo	S6 Cerrito Piñón	S7 La Rinconada	S8 Catan Lil	S9 Mendaña	S10 Collón cura
Taxa	$n = 58$	$n = 103$	$n = 107$	$n = 34$	$n = 33$	$n = 28$	$n = 63$	$n = 28$	$n = 90$	$n = 6$
Small mammals	72.3	65.6	64.1	37.3	48.2	48.9	55.3	52.6	46.2	49.1
Lagomorphs	0.0	4.5	0.0	37.3	12.5	26.7	9.7	17.5	15.4	5.7
Birds	4.8	5.1	4.7	3.9	16.1	6.7	11.7	3.5	15.4	1.1
Reptiles	3.6	7.0	5.9	13.7	12.5	15.6	21.4	12.3	23.1	30.3
Arthropods	19.3	17.8	25.3	7.8	10.7	2.2	1.9	14	0.0	13.7

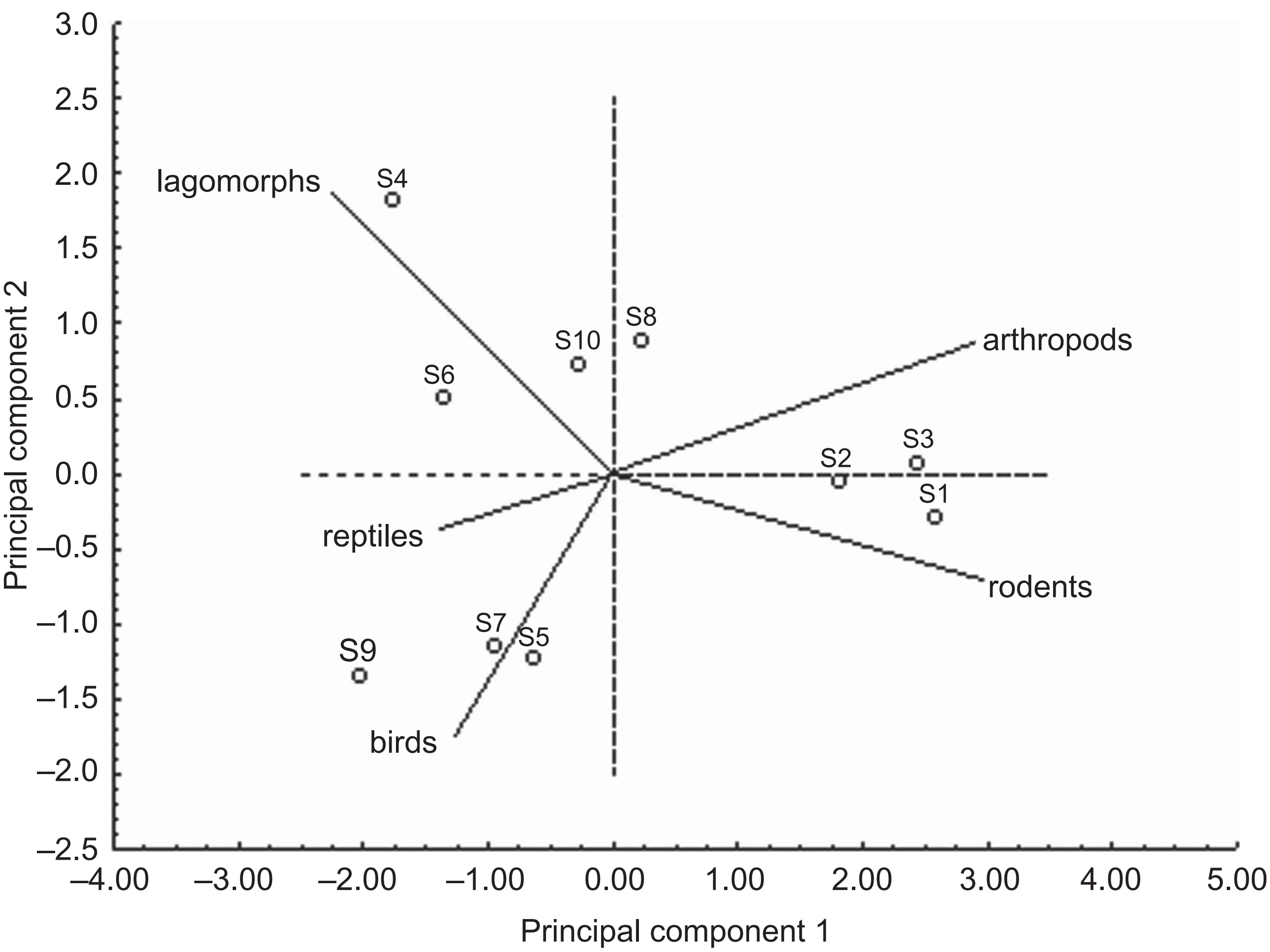

Figure 3. Principal component analysis (PCA) of the diet of the Red-backed Hawk in the different sampling sites of two localities from northwestern (S4 to S10) and southern (S1 to S3) Patagonia. For names of the sites see Methods.

of hares they can prey on. Nevertheless, hawks were seen consuming adult hares as carrion (A. Travaini, M. Santillan, S. Zapata, personal observations), so we speculate that in spite of being limited by hare size, hares of all sizes were abundant, at least during their breeding season, so that they were consumed according to their availability, thereby affecting the hawks' prey selection.

Finally, it is important to be alert to the consequences of introduced species in fragile habitats such as the Patagonian steppe (Novillo & Ojeda 2008, Merino et al. 2009), with extreme situations such as favoring native predator abundance (Bertonatti & Corcuera 2000) and the reorganization of complete predator assemblages into trophic guilds based on the consumption of the new species, i.e. the European hare (Travaini et al. 1996, Zapata et al. 2007).

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