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Dietary overlap of coexisting exotic brown hare (*Lepus europaeus*) and endemic mara (*Dolichotis patagonum*) in Northern Patagonia (Mendoza, Argentina)

Abstract: Introduced brown hares are present across the distribution range of maras, which are endemic to Argentina's open steppes. Food competition with exotic herbivores could be partially responsible for declines in mara populations. Diets of sympatric hares and maras were compared to detect dietary overlap according to food availability. Diets and availability were estimated using microhistological analysis and point-quadrat transects, over four seasons. Horn's index estimated dietary overlap, Kruskal-Wallis ANOVA detected significant differences, and permutational multivariate analysis of variance (PERMANOVA) determined the multivariate response to factors. Grasses prevailed among available items and in both diets. Plant cover and richness increased in summer and forbs in spring. High dietary overlap decreased in autumn-winter, when hares ate more forbs and tall shrubs and less low shrubs than maras. Interspecific overlap was higher inside a protected area with higher food diversity, more forbs, and low shrubs. Both herbivores shifted to different foods as availability decreased. When forbs declined, they were less eaten by maras than hares. Broader habitat use allows hares to search for preferred forbs farther away than maras. The more adaptive hare could become a stronger competitor in impacted environments. Better food availability inside than outside the protected area is a feeding advantage for the coexistence of these herbivores.

Keywords: arid environments; Caviidae; feeding ecology; Leporidae; resource partitioning.

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Introduction

The brown hare (*Lepus europaeus* Pallas 1837; Order Lagomorpha, Family Leporidae) is considered one of the most widespread mammal species in the world. Introduced in South America from Germany and France, the brown hare arrived in Argentina in 1888 (Godoy 1963) and dispersed at a rate of 18.6 km/year (Grigera and Rapoport 1983). Today, *L. europaeus* occurs in shrub steppes and Andean deserts as well as in dry and humid forests and wooded savannahs of South America. Its distribution range encompasses almost all of Argentina, Uruguay, and Chile, as well as the south of Peru, Bolivia, Paraguay, and Brazil (Bonino et al. 2008). Several attributes of invasiveness were found for the brown hare, such as high dispersal ability, broad diet, habitat generalism, high reproductive capacity, and a large native range (Novillo and Ojeda 2008).

The successful introduction of an invasive species usually results in disruptive effects and, combined with other human impacts such as habitat destruction and fragmentation, can be responsible for many endemic species becoming extinct or seriously endangered (Brown and Sax 2004). Competition with native herbivores is hypothesized as one of the most likely impacts of the brown hare in South America, where the mara (*Dolichotis patagonum* Zimmermann 1780; Order Rodentia, Family Caviidae), plains viscacha (*Lagostomus maximus* Desmarest 1817), and tapeti (*Sylvilagus brasiliensis* Linnaeus 1758) are considered potential ecological equivalents of *Lepus europaeus* (Novillo and Ojeda 2008). The brown hare's distribution completely overlaps the geographic range of the mara (Taber 1987), an endemic mammal to Argentina's open grasslands and shrubland steppes. The introduction of exotic herbivores like *L. europaeus* was detected as a threat to *Dolichotis patagonum* (Baldi 2004), a species categorized as Near Threatened (Ojeda and Pardiñas 2008). Both species are medium-sized herbivores, with body weights from 2.5 to 7.0 kg for brown hares (Macdonald and Barret 1995) and 8.0 kg for maras

(Taber 1987). Despite some behavioral and ecological differences between maras and brown hares (Taber and MacDonald 1992), interspecific competition for food could be responsible for the decline in mara populations, among other factors, but further conclusive evidence is still needed (Grigera and Rapoport 1983, Bonino et al. 1997).

Resource partitioning among sympatric populations of ecologically similar species allows them to avoid or reduce interspecific competition (Schoener 1974). Evolution in sympatry facilitates species coexistence through niche differentiation, and food use is one of the most important niche components (Schoener 1983, Krebs 1998). Species with independent evolutionary histories had not the chance of achieving resource partitioning to facilitate coexistence, so interspecific competition is more to be expected between native and introduced herbivores than between native herbivores (Kirchhoff and Larsen 1998, Madhusudan 2004), and their dietary overlap is usually higher than among native species (Puig et al. 2006, Davis 2010). Moreover, the theory of maximal tolerable niche overlap predicts higher niche overlap in situations of resource abundance because species can share unlimited food and more highly segregated niches in resource-limited situations, which may respond to strong competition (Pianka 1974).

Brown hares are present across the arid steppes of Northern Patagonia, even in the few habitats occupied by maras. The objective of this study is to compare the diets of sympatric brown hares and maras in two landscapes of Northern Patagonia, in order to detect: a) how important dietary overlap between brown hares and maras is throughout the year and b) whether changes in food availability affect resource partitioning between these herbivores.

Materials and methods

Study area and habitat characteristics

The study area (36°30'S 69°00'W, 1,200 to 2,000 m in altitude) is representative of La Payunia, the northernmost biogeographic unit of the Patagonian province (Cabrera and Willink 1980), which has recently been proposed as a new phytogeographic province (Martínez Carretero 2004). The climate is continental desert (Consejo Federal de Inversiones 1977). Mean temperature ranges from 6°C in winter to 20°C in summer, and annual precipitation averages 255 mm. The relief presents gentle slopes and large

plains, interrupted by basaltic steps and hills of volcanic origin (González Díaz 1972, 1979). The xerophilous vegetation is shrub steppe, where almost all shrub species are evergreen.

Two study sites, corresponding to different landscapes (González Díaz 1972, 1979, Martínez Carretero and Dalmaso 1993), were selected based on the stable presence of maras, as these caviomorphs are sparsely distributed in the study area (Puig et al. in prep.). One sampling site was located within the old peneplain of Huayquerías, co-dominated by open shrublands and grasslands (Martínez Carretero and Dalmaso 1993, Abraham 2000). The other sampling site was within the plateau and piedmont surrounding the Sierras de Chachahuén (2065 m a.s.l.), dominated by sandy grassland with patches of lithosol scrubland (Roig et al. 1996, Abraham 2000). Puig et al. (2010) has a more detailed description of these landscapes. Poaching, fire, woody plant removal, road opening, mining, and oil extraction affect the Chachahuén area, situated outside the Payunia Reserve, more intensely than they affect Huayquerías, a landscape belonging to this protected area (Candia et al. 1993).

Field and laboratory design

Samplings were conducted seasonally during 2005–2006, i.e., during spring (October), summer (January), autumn (April), and winter (July). At each occasion, 40 fecal samples of brown hares and 40 fecal samples of maras were collected from each sampling site, and 40 transects were traversed to estimate plant cover and relative frequencies of plant species with the point-quadrat method (Daget and Poissonet 1971). All 30-m transects (100 points per transect) were randomly distributed within each sampling site, separated from each other by more than 100 m. Fecal samples were collected from 10 groups of fresh feces per herbivore at each sampling site. Each fecal sample, composed of 10 fresh pellets, was collected from a different group of feces. After being oven-dried at 60°C, each sample was milled, cleared with diluted lye (aqueous sodium hypochlorite, 25% w/v), and passed through a sieve. Fecal samples were analyzed following the microhistological method of Baumgartner and Martin (1939), modified by Duci (1949) and Holechek (1982), using reference plant material from La Payunia region identified by Puig et al. (1996) and new reference plant material collected and identified during the present study, both stored in the Ruiz Leal Herbarium (IADIZA, Argentina). Plant cuticle

was identified to genus level and to species level when possible.

Statistical analyses

Plant cover was determined for each point-quadrat transect by dividing the number of points at which any plant species was contacted (except dead individuals) by the 100 transect points. Relative frequency of a given plant species in the environment was determined by dividing the absolute frequency of this species by the total sum of absolute frequencies for all species identified along each transect. Only those plant species consumed on at least one occasion by brown hares or maras were considered in the analyses of food availability. The relative frequency of a given species in the diet was determined for each sample by dividing the number of microscopic fields where that species was observed by the number of fields for all observed species (Holeček and Gross 1982). Plant species with proportions of more than 0.05 were considered food items of frequent use.

Plant species were grouped into four categories according to life form: grasses, forbs, low shrubs, and tall shrubs. Diversity in food availability and diet was estimated using the Shannon-Wiener function (Colwell and Futuyma 1971). Dietary overlap between brown hares and maras was estimated using Horn's index (Horn 1966), which is based on information theory, is little affected by sampling size, and is therefore considered the best measure of overlap when resource use is expressed as proportions (Krebs 1989). Significant spatial and temporal differences in diets and food availability were detected with Kruskal-Wallis ANOVA and multiple comparisons of mean ranks for all groups (Siegel and Castellan 1988). A multivariate comparison of diets was done with canonical redundancy analysis (Rao 1964), considering as response variables the frequency matrix of plant species (excluding rare ones), previously transformed with the Hellinger method (Legendre and Gallagher 2001), and herbivore species, season, and sampling site as potential explanatory variables. Permutation tests for homogeneity of multivariate dispersions (Anderson 2006), Hellinger distance-based, were conducted, and then permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) was applied to detect significant dietary differences. These analyses were performed with R software 2.15.2 version (R Foundation for Statistical Computing, Vienna, Austria; R Development Core Team 2008) and the "vegan" package developed at R-Forge, maintainer J. Oksanen, Oulu Univ., Finland; (Oksanen et al. 2008). The level of significance obtained was mostly $p \leq 0.001$; otherwise, it is mentioned in the text.

Results

Food availability for both herbivores

About half of the 38 species found at the sampling sites were used on at least one occasion by brown hares or maras (Table 1). The grass category accounted for more than 80% of total availability (Table 2), followed by low and tall shrubs (9% and 7%, respectively). The main species available on both sampling sites were the grasses *Panicum urvilleanum* and *Poa* spp., additionally the tall shrub *Neosparton aphyllum* in Huayquerías (Figure 1).

The study area had the lowest plant cover in winter (Table 3), when low shrubs and the grass *Stipa* spp. presented higher relative proportions than in other seasons. Plant cover increased in spring, along with the proportion of the grass *Poa* spp. In addition, the proportion of forbs (mainly *Plantago patagonica*) showed a spring increase in Huayquerías. The highest plant cover occurred in summer-autumn, with a greater number of available species in summer than in autumn, and a higher proportion of the grass *Panicum urvilleanum* in autumn.

A similar plant cover (79%) was estimated for both sampling sites. Available food was more diverse in Huayquerías than in Chachahuén (Table 3), with higher richness, a higher proportion of low shrubs (mainly *Baccharis darwini*), a lower proportion of grasses (mainly *Poa* spp.), and, during summer, a higher proportion of forbs (mainly *Plantago patagonica*). Compared with Chachahuén, Huayquerías showed a higher proportion of the grass *Stipa* spp. and a lower proportion of the low shrub *Hyalis argentea*.

Characterization of both herbivore diets

The diets of brown hares and maras showed a similar number of plant species (18 and 20 species, respectively). Grasses made up more than 80% of each herbivore's diet, followed by tall shrubs and forbs in the brown hare's diet and by low shrubs in the mara's diet (Table 2). Among the grasses, the *Poa* spp. constituted about 50% of both. Other main species in both diets were the grasses *Bromus catharticus* and *Panicum urvilleanum*, also *Stipa* spp. and the low shrub *Prosopis alpataco* in the mara's diet (Figure 1).

The proportion of grasses increased in spring in the brown hare's diet and during spring-summer in the mara's diet (Table 3). Tall shrubs comprised a higher proportion of the brown hare's diet during autumn-winter (more strongly in Chachahuén than in Huayquerías), also the proportion

Table 1 Scientific names, authorities, and acronyms for the plant species included in the diets (X) of the brown hare *Lepus europaeus* (HA) and the mara *Dolichotis patagonum* (MA) at the sampling sites in Northern Patagonia.

Scientific name	Authority	Acronym	HA	MA
Grasses				
<i>Bromus catharticus</i>	Vahl 1791	Bc	X	X
<i>Eragrostis pilosa</i>	(L.) P. Beauv. 1812	Ep		X
<i>Panicum urvilleanum</i>	Kunth 1831	Pu	X	X
<i>Poa</i> spp.	L. 1753	Ps	X	X
<i>Schismus barbatus</i>	(L.) Thell. 1907	Sb		X
<i>Sporobolus rigens</i>	(Trim.) E. Desv. 1854	Sr	X	X
<i>Stipa</i> spp.	L. 1753	Ss	X	X
Forbs				
<i>Doniophyton</i> spp.	Wedd. 1855	Ds		X
<i>Hoffmannsegia</i> aff. <i>glauca</i>	(Ortega) Eifert 1972	Hg	X	X
<i>Lecanophora ameghinoi</i>	(Speg.) Speg. 1926	La	X	X
<i>Plantago patagonica</i>	Jacq. 1795	Pp	X	X
<i>Sphaeralcea mendocina</i>	Phil. 1862	Sm		X
Low shrubs				
<i>Acantolippia seriphioides</i>	(A Gray) Moldenke 1940	As	X	X
<i>Atriplex lampa</i>	(Moq.) D. Dietr. 1852	Al	X	
<i>Baccharis darwini</i>	Hook. & Arn. 1841	Bd	X	X
<i>Hyalis argentea</i>	D. Don ex Hook. & Arn. 1835	Ha	X	X
<i>Junellia</i> spp.	Moldenke 1940	Ja	X	X
<i>Prosopis alpataco</i>	Phil. 1862	Pa		X
<i>Senecio filaginoides</i>	DC. 1838	Sf	X	
Tall shrubs				
<i>Chuquiraga erinacea</i>	D. Don (Don) C. Ezcurra 1985	Ce	X	X
<i>Lycium chilense</i>	Miers ex Bertero 1829	Lc	X	X
<i>Neosparton aphyllum</i>	(Gillies & Hook. ex Hook.) Kuntze 1898	Na	X	
<i>Prosopidatrum globosum</i>	(Gillies ex Hook. & Arn.) Burkart 1964	Pg	X	X

Table 2 Diversity and composition of food availability and diets of the brown hare *Lepus europaeus* and the mara *Dolichotis patagonum* during winter (Win), spring (Spr), summer (Sum), and autumn (Aut) at the sampling sites in Northern Patagonia.

	Huayquerías				Chachahuén			
	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut
Food availability								
Plant cover (%)	62	76	90	87	65	75	90	84
Species diversity	0.57	0.60	0.62	0.53	0.52	0.49	0.48	0.47
Species richness (frequent spp.)	8 (5)	8 (4)	9 (4)	7 (3)	6 (3)	7 (3)	7 (2)	6 (3)
Grasses	0.72	0.80	0.78	0.81	0.83	0.86	0.90	0.87
Forbs	<0.01	0.07	0.04	<0.01	<0.01	0.02	<0.01	<0.01
Low shrubs	0.16	0.07	0.11	0.10	0.10	0.05	0.05	0.08
Tall shrubs	0.12	0.05	0.07	0.09	0.07	0.07	0.04	0.05
Diet of the brown hare								
Species diversity	0.63	0.57	0.59	0.64	0.56	0.6	0.62	0.62
Species richness (frequent spp.)	14 (3)	10 (3)	12 (4)	12 (3)	9 (3)	10 (4)	14 (5)	12 (3)
Grasses	0.82	0.92	0.88	0.86	0.83	0.92	0.87	0.80
Forbs	0.10	0.07	0.08	0.11	<0.01	<0.01	0.07	0.02
Low shrubs	0.02	<0.01	<0.01	<0.01	0.06	0.02	0.03	0.03
Tall shrubs	0.06	0.01	0.03	0.02	0.12	0.06	0.03	0.15
Diet of the mara^a								
Species diversity	0.53	0.61	0.62	0.56	0.52	0.46	0.56	0.55
Species richness (frequent spp.)	9 (3)	13 (3)	11 (5)	11 (3)	6 (4)	11 (4)	10 (5)	13 (4)
Grasses	0.88	0.84	0.88	0.82	0.79	0.95	0.91	0.79
Forbes	0.04	0.08	0.05	0.02	<0.01	0.02	<0.01	<0.01
Low shrubs	0.04	0.02	0.02	0.03	0.21	0.01	0.08	0.20
Tall shrubs	0.05	0.06	0.05	0.12	0.00	0.02	0.01	0.01

^aValues for mara's diet are drawn from Puig et al. (2010).

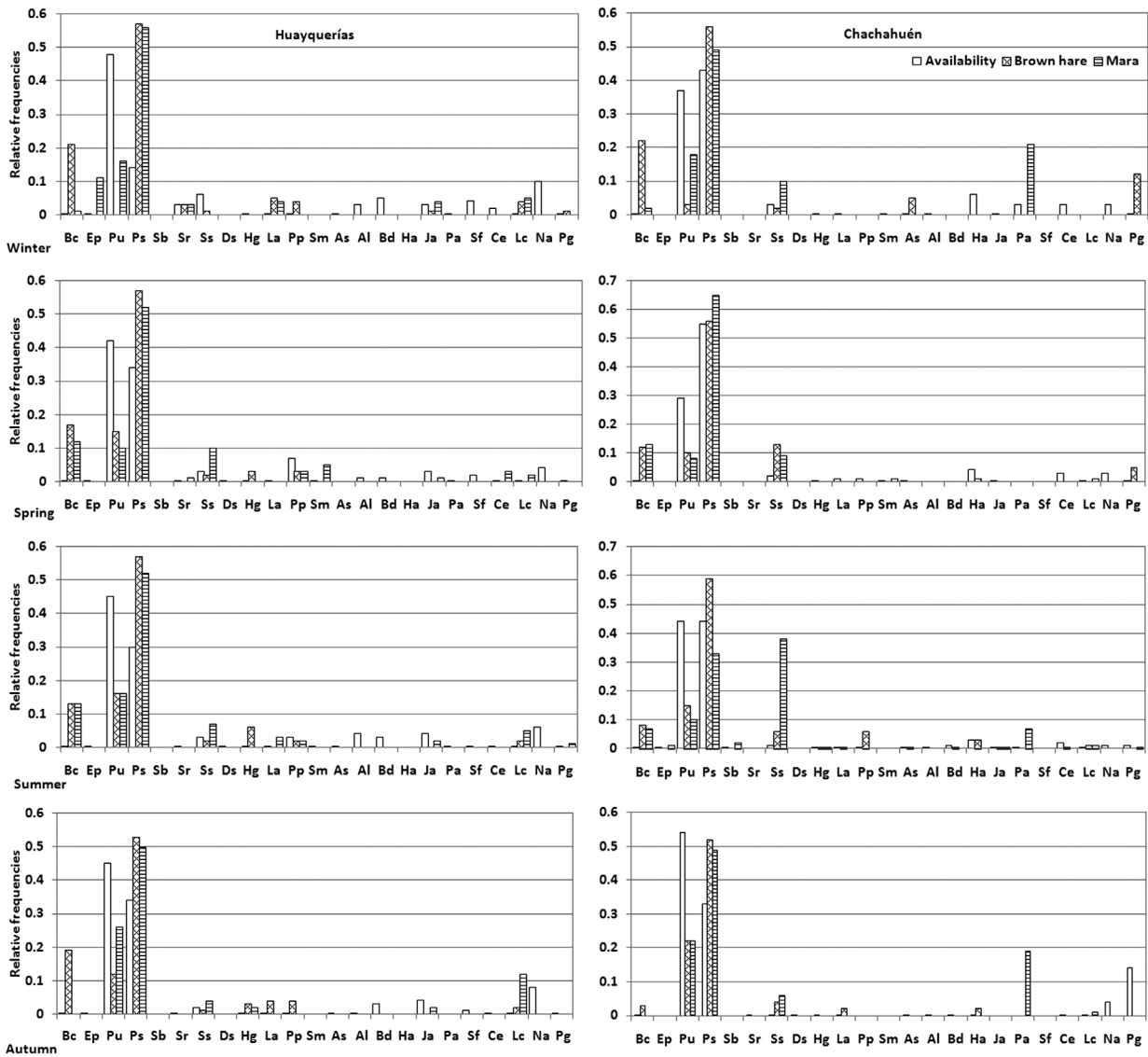


Figure 1 Proportion of plant species in environmental food availability and diets of the brown hare *Lepus europaeus* and the mara *Dolichotis patagonum* during winter (Win), spring (Spr), summer (Sum), and autumn (Aut) at the sampling sites in Northern Patagonia. Values for the mara's diet are drawn from Puig et al. (2010). Species identifications are in Table 1.

of the tall shrub *Lycium chilense* increased in autumn in the mara's diet in Huayquerías. Besides, the autumn-winter diet of maras showed a strong increase in the proportion of low shrubs, particularly *Prosopis alpataco* in Chachahuén. The proportion of the forb *Lecanophora ameghinoi* increased in the winter diet of brown hares.

Dietary differences between brown hares and maras

Despite no significant differences shown by dietary diversity between herbivores in any season or for any

sampling site, several plant species were exclusively used by maras or brown hares (Tables 1 and 2). Only the mara's diet included the grasses *Eragrostis pilosa* and *Schismus barbatus*, the forbs *Doniophyton* spp. and *Sphaeralcea mendocina*, and the low shrub *Prosopis alpataco*. Some of these nonshared species were frequently used by maras in Huayquerías (*E. pilosa* in winter and *S. mendocina* in spring), and in Chachahuén (*P. alpataco* almost all year round) (Figure 1). Only the brown hare's diet included the low shrubs *Atriplex lampa* and *Senecio filagonoides*, and the tall shrub *Neosparton aphyllum*. None of these nonshared species was frequently used by brown hares.

Table 3 Food availability differences among seasons and between the sampling sites, Huayquerías (HU) and Chachahuén (CH), and seasonal changes in the diets of brown hares and maras.

	Differences in food availability		Seasonal changes in the diets	
	Seasonal	Spatial	Brown hares	Maras
Plant cover	H=53.86			
Richness	H=10.97 p=0.012	H=19.62		
Diversity		H=21.78		
Grasses		H=20.24	H=14.61 p=0.002	H=19.09
<i>Panicum urvilleanum</i>	H=13.56 p=0.004			
<i>Poa</i> spp.	H=10.68 p=0.014	H=18.67		
<i>Stipa</i> spp.	H=15.29 p=0.002	H=15.81		
Forbs	H=22.46 HU:H=22.71	H=6.39 p=0.012 Sum: H=11.54		
<i>Lecanophora ameghinoi</i>			H=15.73	
<i>Plantago patagonica</i>	H=23.62, HU: H=21.38	Sum: H=12.91 p=0.003		
Low shrubs	H=9.81 p=0.020	H=10.45		H=20.49
<i>Atriplex lampa</i>		H=24.40		
<i>Baccharis darwini</i>		H=25.78		
<i>Hyalis argentea</i>		H=60.01		
<i>Junellia</i> spp.		H=16.22		
<i>Prosopis alpataco</i>				CH: H=27.23
<i>Senecio filaginoides</i>		H=38.07		
Tall shrubs			H=16.16 CH:H=16.46 HU:H=10.81 p=0.013	
<i>Lycium chilense</i>				HU: H=23.12

Sum, spatial differences particularly in summer; H, the value of Kruskal-Wallis test.

The dietary proportion of grasses did not differ between these herbivores (Tables 2 and 4). In terms of shared grasses (Figure 1), the brown hare's diet differed from the mara's diet due to higher proportions of *Bromus catharticus* (especially in autumn-winter) and *Poa* spp. (mainly in summer in Chachahuén) and lower proportions

of *Stipa* spp. (mostly in summer-autumn) and *Panicum urvilleanum* (especially in autumn-winter).

The dietary proportion of forbs was higher for brown hares than for maras (mostly in autumn-winter at both sites). With regard to shared forbs, the brown hare's diet differed from the mara's diet by containing higher

Table 4 Dietary differences between brown hares and maras, at both or one of the sampling sites Huayquerías (HU) and Chachahuén (CH).

	Annual	Winter	Spring	Summer	Autumn
Grasses					
<i>Bromus catharticus</i>	H=35.53	H=23.68			H=24.89
<i>Panicum urvilleanum</i>	H=9.03 p=0.003	H=26.45			H=7.24 p=0.007
<i>Poa</i> spp.	H=6.53 p=0.011			CH: H=8.92 p=0.003	
<i>Stipa</i> spp.	H=16.13			H=12.73	H=5.83 p=0.016
Forbs	H=9.20 p=0.002	H=5.16 p=0.023			H=11.24
<i>Hoffmannsegia glauca</i>	H=13.54		HU: H=7.82 p=0.005	HU: H=7.82 p=0.005	
<i>Lecanophora ameghinoi</i>	H=9.91 p=0.002				H=17.57
<i>Plantago patagonica</i>	H=13.37	HU: H=7.82 p=0.005			HU: H=13.86
Low shrubs	H=25.90				
<i>Acantholippia seriphioides</i>		CH: H=11.65			
<i>Hyalis argentea</i>	H=12.05			CH: H=9.64 p=0.002	CH: H=9.38 p=0.002
<i>Junellia</i> spp.	H=6.37 p=0.012		HU: H=10.64		
Tall shrubs		CH: H=14.40			CH: H=13.86
<i>Lycium chilense</i>					HU: H=14.35
<i>Prosopidastrum globosum</i>		CH: H=13.86			CH: H=16.32

H stands for the value of Kruskal-Wallis test.

proportions of *Hoffmannseggia* aff. *glauca* (mostly during spring-summer in Huayquerías), *Plantago patagonica* (mostly in autumn-winter in Huayquerías), and *Lecanophora ameghinoi* (especially in autumn at both sites).

Brown hares showed a lower dietary proportion of low shrubs than maras throughout the year at both sampling sites. Regarding shared low shrubs, the brown hare's diet differed from that of the mara by having higher dietary proportions of *Hyalis argentea* (mainly in summer-autumn in Chachahuén) and *Acantholippia seriphioides* in winter in Chachahuén.

The proportion of tall shrubs in the brown hare's diet was higher than in the mara's diet in Chachahuén during autumn-winter (particularly for *Prosopidastrum globosum*), but it was lower in Huayquerías for *Lycium chilense* during autumn.

The PerMANOVA applied to all cases ($n=160$) of relative frequencies of plant species showed significant differences for each factor and its interactions. The main sources of the total explained variance (60%) were the type of herbivore, season, and the interaction between them ($R^2=0.13$, 0.12, and 0.11, respectively). Sampling site and its interactions with the other explanatory variables were less important but also significant ($R^2=0.09$ for site, 0.05 for herbivore:site and season:site, 0.06 for site:season:herbivore). Owing to interaction significance, the diets were analyzed separately ($n=20$) for each season and sampling site with PerMANOVA, after corroboration of homogeneity of multivariate dispersion between herbivores in each condition. Percentages of explained variance were higher in autumn-winter, and more similar between sampling sites, than in spring-summer (Figure 2). During autumn-winter, both herbivores were associated to different grasses (*Bromus catharticus* for hares, *Panicum urvilleanum* for maras), followed by different shrubs (*Prosopidastrum globosum* for hares, *Prosopis alpataco*, and *Lycium chilense* for maras). During spring-summer there was a weak association of both herbivores with several grasses and forbs, with the exception of the summer association of maras with the grass *Stipa* spp. in Chachahuén.

Dietary overlap and food items shared between brown hares and maras

Brown hares and maras shared the use of 15 of the 23 plant species included in their diets (five of the seven grasses, three of the five forbs, four of the seven low shrubs, and three of the four tall shrubs). Four of the shared grasses were frequently used by both herbivores: *Poa* spp. and *Panicum urvilleanum* throughout the year, *Bromus*

catharticus and occasionally *Stipa* spp. in spring-summer (Figure 1). The mean number of food items shared between brown hares and maras was higher in spring-summer than in autumn-winter, at both sampling sites (Figure 3B, $H=30.04$, in Huayquerías $H=15.37$ $p=0.002$ and in Chachahuén $H=16.67$). These seasonal changes were detected also for those items frequently used by both herbivores ($H=35.98$, in Huayquerías $H=19.37$ and in Chachahuén $H=21.77$). Additionally, the mean number of shared items was higher in Huayquerías than in Chachahuén ($H=4.91$ $p=0.027$).

Dietary overlap between herbivores was considerably high at both sampling sites, estimated in plant categories (97% in Huayquerías, 94% in Chachahuén) and in plant species (85% in Huayquerías, 80% in Chachahuén). Dietary overlap of plant species was higher in spring-summer than in autumn-winter (Figure 3A, $H=29.36$; in Huayquerías $H=22.61$ and in Chachahuén $H=20.38$), also the overlap of plant categories was higher in spring-summer than in autumn ($H=16.46$, particularly in Chachahuén $H=14.83$ $p=0.002$). Dietary overlap of plant species was higher in Huayquerías than in Chachahuén during summer ($H=8.69$ $p=0.003$).

Discussion and conclusion

The brown hare and the mara showed dietary generalism, as their diets included about half of the plant species present in the environment. Brown hares also showed dietary generalism in other landscapes of Northern Patagonia (Puig et al. 2007). Generalism favors the survival of species in environments where food is a limiting resource, for it enhances their ability to shift among food items (Schleuter and Eckmann 2007). Despite this generalism, grasses comprised more than 80% of the diets of both herbivores, allowing their classification as "grazers" according to the feeding classes defined by Bothma et al. (2004). The low availability of shrubs in the studied landscapes could constrain the use of this food resource by brown hares and maras. In fact, tall shrubs made up 21% of the brown hare's diet in other landscapes of Northern Patagonia (Puig et al. 2006), where this plant category showed twice the availability observed at the current study sites. In shrub landscapes of the Central Monte, the diet of the brown hare included higher proportion of dicots than the mara's diet (Campos et al. 2001). On the other hand, in a scrubland of evergreen bushes of the Southern Monte, shrub species made up half of the diets of both maras and brown hares, and a considerable

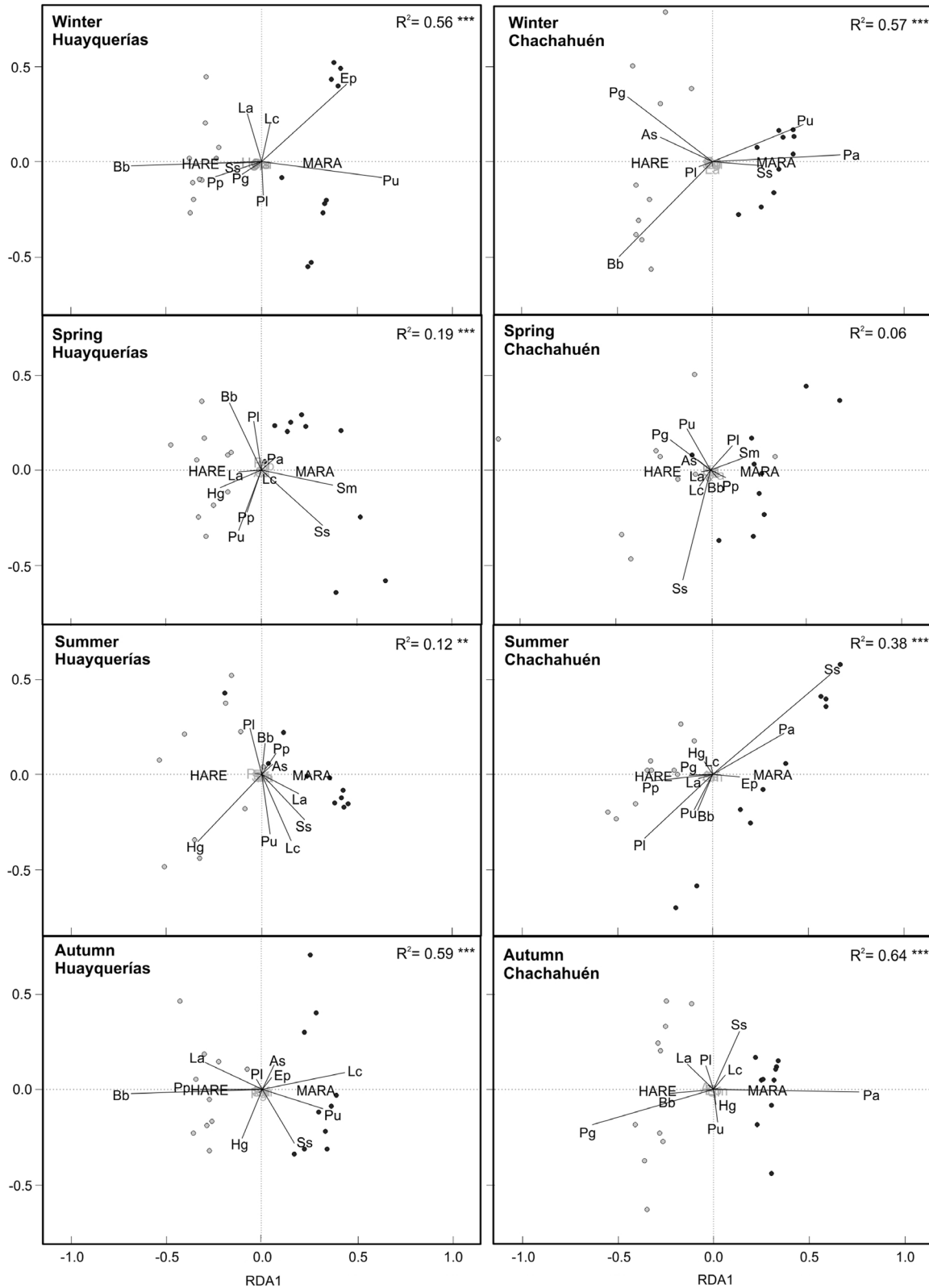


Figure 2 PerMANOVA triplots (scaling 2) using the first canonical axis (RDA1) and the first axis of residuals (PCA1) for each season and sampling site, with adjusted R² and its significance level: p<0.001 (***) and p<0.01 (**). The name of each herbivore indicates the location of the respective centroid. Black circles correspond to mara's samples and gray circles to samples of brown hares. Plant species identifications are in Table 1.

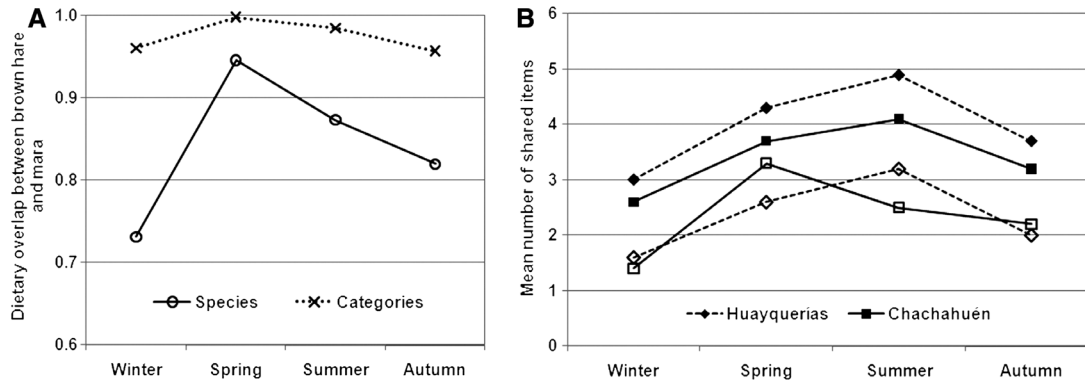


Figure 3 Dietary overlap between the brown hare *Lepus europaeus* and the mara *Dolichotis patagonum* at the sampling sites in Northern Patagonia throughout the year (A), and mean number of food items shared by both herbivores (B) considering all items shared (filled dots) and items frequently used by both herbivores (empty dots).

dietary overlap was found between these herbivores (Bonino et al. 1997). A similar interspecific overlap was found in an open Mesquite shrubland of the Northern Monte, where shrubs dominated the diets of both herbivores (Reus et al. 2013).

The expected high dietary overlap between brown hares and maras was confirmed in the study landscapes of Northern Patagonia, reinforced by the similarity found in their diets in terms of diversity, richness, prevalence of grasses, same main species (especially *Poa* spp., also *Panicum urvilleanum* and *Bromus catharticus*), by a spring increase in the proportion of grasses in both diets and by the fact that brown hares and maras shared most of the species included in their diets. The case studied here of brown hares and maras agrees with the prediction of a more important overlap between exotic-native herbivores than between native-native herbivores. Indeed, the mean diet overlap between brown hare and mara was found to be considerably high (83%) compared to the overlap between mara and other native herbivores present in this environment (69%) (Puig et al. 2006).

Changes in diet composition and interspecific overlap are expected in the study environment, in response to characteristic temporal and spatial changes in food availability for herbivores (Puig et al. 1996, 2010). The theory of maximum tolerable niche overlap (Pianka 1974, Schoener 1982) predicts stronger efforts to reduce dietary overlap as food becomes scarcer and as competition for this resource increases. The number of food items shared between brown hares and maras and their diet overlap concurred with this prediction, as both estimates were higher in seasons with favorable feeding conditions (spring-summer) than in seasons with resource-limited conditions (autumn-winter). Increased plant cover, a

higher availability of forbs and of the grasses *Poa* spp. and *Panicum urvilleanum*, major food items for brown hares and maras, constituted favorable conditions for these herbivores in spring-summer. Resource-limited conditions in autumn-winter included not only grass senescence but also decreased food richness and plant cover. Additionally, the number of food items shared between brown hares and maras and their diet overlap were higher in the landscape with more favorable feeding conditions (Huayquerías). Chachahuén, the other landscape, presented comparatively more limited food availability than Huayquerías in terms of lower diversity, richness, proportion of forbs in summer, and proportion of low shrubs.

A different response to food scarcity was observed in brown hares and maras, contributing to partially segregate their niches especially in the most resource-limited situation (autumn-winter in Chachahuén). Each herbivore increased the use of different food types: tall shrubs for brown hares and low shrubs (especially *Prosopis alpataco*) for maras. The high nitrogen concentration in *P. alpataco* (Campanella and Bertiller 2008) would be responsible for the mara's preference for this shrub species during the seasonal decline in forbs and grasses. Furthermore, the mara became a "mixed feeder," according to classes defined by Bothma et al. (2004), preferring *P. alpataco* and other shrubs during an extended drought in Northern Patagonia (Puig et al. 2010), and the same occurred in other mara populations in the dry season (Kufner et al. 1992, Campos et al. 2001, Sombra and Mangione 2005). Brown hares and maras also showed a different response to the limited resources in the dry season (winter) in an open Mesquite shrubland of the Northern Monte, for the diet of maras had a stronger decrease in diversity, including a higher proportion of cactaceae and

a lower proportion of shrubs than the hare's diet (Reus et al. 2013).

The seasonal decrease in forbs in the vegetation seems to affect the mara more than it affects the brown hare, given that the dietary proportion of forbs was lower for maras than for brown hares during autumn-winter. The wider habitat use attributed to brown hares (Kufner et al. 2008) could help them maintain the use of their preferred foods, like forbs, for they can search for them farther away than maras can. The mara appears to be a central-place forager, at least during the long reproduction period (Ganslosser and Wehnelt 1997) when it remains near warrens built in open grass-dominated habitats (Taber 1987, Baldi 2004). The brown hare usually moves among habitats according to food and shelter availability (Tapper and Barnes 1986), it rests in depressions without building burrows, and has a shorter breeding period than the mara (Dubost and Genest 1974, Bonino 2007).

A more relaxed interspecific situation seems to occur when resources become relatively less scarce, given that the dietary overlap was higher in spring-summer, and the proportion of grasses increased in diets of both herbivores. Despite the better conditions of spring-summer, compared to the scarcity in autumn-winter and the extended drought periods, food is clearly a limited resource taking into account its low availability, strongly affected by temporal and spatial uncertainty of rainfall (Puig et al. 1996, 2010). Therefore, the explanation postulated by Pianka (1974) that high interspecific overlap occurs because there are nonlimited food resources for herbivores does not apply in this case. A certain level of differentiation in spatial or temporal niche components is another alternative to explain high dietary overlap (Pianka 1981). Although maras have a restricted habitat use due to their association with bare ground (Rodríguez 2009), spatial differentiation is not possible because brown hares are generalists in their use of habitat (Tapper and Barnes 1986). Partial differentiation in the temporal niche, as maras are diurnal and hares concentrate their activities during evening-night hours (Taber 1987, Bonino 2007), has no influence on the fact that these herbivores have to share food.

The high overlap between brown hare and mara, compared to the overlap between mara and other native herbivores present in the study environment, agrees with the prediction that the native-exotic overlap will be higher than the native-native overlap, considering niche differentiation as a consequence of evolution in sympatry (Schoener 1983). This pattern was also detected for other herbivore assemblages (Kirchhoff

and Larsen 1998, Voeten and Prins 1999, Madhusudan 2004). In synthesis, the most acceptable explanation for the high dietary overlap between mara and brown hare is that they are, respectively, a native and an exotic species that have not evolved in sympatry with each other, whereas the other potential explanations were not sustained by the food scarcity characteristic of this arid environment and the brown hare's generalism in the use of habitats.

Feeding advantages for the coexistence of maras and brown hares are related to the better conservation conditions inside than outside the Payunia protected area (Huayquerías and Chachahuén landscapes, respectively). Indeed, dietary overlap and number of shared species were higher in Huayquerías, where food availability showed higher diversity and richness. Increasing human impacts, such as oil extraction and mining, damage the environment in Chachahuén (Novaro 2004). Vegetation clearing and fragmentation, derived from human activities, and the mara's preference for bare ground could lead it to select these risky sites in terms of poaching or food depletion from livestock overgrazing (Kufner and Chambouleyron 1991, Baldi 2007, Rodríguez, 2009). The ecological trap hypothesis (Dwernychuk and Boag 1972) has been suggested to explain the mara's selection of human-modified sites (Rodríguez 2003). The brown hare, less vulnerable than the mara due to a more adaptive use of resources, could become a stronger competitor in impacted environments.

Ongoing studies on habitat selection by brown hares and maras in Northern Patagonia are expected to complement the current research, with the aim to integrate both components, habitat and food, in the discussion about interspecific niche partitioning, and to assess the effects of human activities on the coexistence of the endemic mara and the exotic brown hare.

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