*Trophic interactions between two medium-sized mammals: the case of the native* Dolichotis patagonum *and the exotic* Lepus europaeus *in a hyper-arid ecosystem*

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# Trophic interactions between two medium-sized mammals: the case of the native *Dolichotis patagonum* and the exotic *Lepus europaeus* in a hyper-arid ecosystem

María L. Reus · Begoña Peco · Claudia de los Ríos · Stella M. Giannoni · Claudia M. Campos

**Abstract** As medium-sized herbivores, the exotic *Lepus europaeus* (European hare) and the native *Dolichotis patagonum* (mara) have been considered ecological equivalents. These species coexist in Ischigualasto Provincial Park, a hyper-arid ecosystem with scarce food resources. Our objective was to evaluate diet composition, relationship between diets and food availability, and trophic relationships between both herbivores. Collection of feces and vegetation sampling were made in the Mesquite woodland community. Diet composition was analyzed by microhistological analysis of feces. In both seasons, shrub species represented the most abundant cover type in the area, and annual forbs and grasses appeared in the wet season. Herbivores showed similar dietary ecology: shrubs were the main food items along the year, showing a higher plasticity compared to their diets in other ecosystems, where they selected mostly grasses. The mara selected shrubs such as *Atriplex* sp. and *Prosopis torquata*, whereas the European hare selected *Cyclolepis genistoides*, *Atriplex* sp., and *Bulnesia retama*. During the wet season, both herbivores supplemented their diets with grasses and annual forbs. In the dry season, there was increased consumption of cacti, such as *Tephrocactus* sp. The mara and the European hare are likely close ecological equivalents, in terms of dietary similarity, and they showed strong dietary overlap across the dry season (over 60 %). Thus, we can assume the existence of a potential trophic competition between mara and European hare, especially during the season when food resources are scarce. These results can be important for the management of drylands in South America, where populations of threatened herbivorous species, such as the mara, coexist with exotic animals, sharing spatial and trophic resources even in protected areas.

**Keywords** Diet overlap · Diversity · European hare · Mara

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## Introduction

Information on species' diets is vital in understanding ecological relationships, particularly when exotic species are involved, because this information allows assessing their potential impacts on ecosystem components (Litvaitis et al. 1996). Competitive interactions and niche overlap can occur between species that use the same resource in similar ways (Colwell and Futuyma 1971), like for example when morphologically similar and phylogenetically closely related species are sympatric (Schoener 1974; Loveridge and Macdonald 2003; DiBitetti et al. 2009). Particularly in arid

lands, where rainfall is unpredictable and markedly seasonal, food and habitat are the main limiting resources for the coexistence of herbivores (Whitford 2002).

*Dolichotis patagonum* (mara) is a rodent endemic to Argentina. It occurs in the ecoregions of Dry Chaco, Espinal, Patagonian steppe, and Monte (Barquez et al. 2006). Its diet varies across its geographic distribution, and it has been characterized as a generalist herbivore with a high preference for grasses (60–80 % in diet; Kufner and Pelliza de Sbriller 1987; Bonino et al. 1997; Campos et al. 2001a; Sombra and Mangione 2005; Rodríguez and Dacar 2008; Chillo et al. 2010). In the Monte Desert, the mara has a large dietary overlap with *Lagostomus maximus* (plains vizcachas), livestock (Kufner and Pelliza de Sbriller 1987; Kufner et al. 1992), and *Lepus europaeus* (Bonino et al. 1997). In the central Monte Desert, the mara consumes leaves of monocots (70 %) and dicots (30 %; Campos 1997). Among grasses, it selects *Chloris*, *Pappophorum*, and *Trichloris*, and among perennial dicots *Atriplex lampa*, *Lycium*, and *Prosopis* (Campos 1997). The mara is also opportunist, feeding on herbs that grow after rainy periods (Kufner and Pelliza de Sbriller 1987). In the southernmost part of the Monte Desert, the diet of the mara is mostly shrubs. Nevertheless, annual and perennial grasses and forbs are also eaten, especially in spring (Bonino et al. 1997).

The mara is listed as vulnerable in Argentina (Ojeda and Diaz 1997; Diaz and Ojeda 2000) and as "near threatened" species in the IUCN Red List (IUCN 2012). Historically, this species occurred from north-central Argentina down south to almost Tierra del Fuego (Rood 1972). However, it has been strongly affected by habitat alteration and hunting, and is locally extinct in some regions, such as Buenos Aires Province (Cabrera 1953). The local population inhabiting the Ischigualasto Provincial Park is considered of "special interest" because of its restricted geographic distribution, its low population density, and the poor basic information about it (Acosta and Murúa 1999).

*Lepus europaeus* (European hare) is widespread in mainland Europe and most common on intensively farmed arable land (Mitchell-Jones et al. 1999; Vaughan et al. 2003). Even though its status has been listed as "least concern" according to the IUCN Red List (IUCN 2012), European hare populations have dramatically declined during recent decades in their original distribution range (Flux and Angermann 1990; Mitchell-Jones et al. 1999; Smith et al. 2005). Despite recent population declines, the European hare has naturalized successfully in many countries including the UK, Sweden, Norway, eastern Canada, north-eastern USA, Australia, New Zealand, as well as in many small islands, and most of South America below 28° South (Flux and Angermann 1990).

The European hare was introduced into central Argentina in 1888 and later on, in 1896, into southern Chilean Patagonia (Grigera and Rapoport 1983). Currently, this species is widespread, and its distribution covers much of Argentina, Chile, Paraguay, Uruguay and southern Brazil, and Bolivia (Grigera and Rapoport 1983). It is a habitat generalist species, highly mobile, adaptable, and it has colonized and invaded different habitats, ranging from meadows to scrubland, steppe, forest clearings, high mountains, and farms (Bonino 1995; Vázquez 2002). This species is able to use low-quality food resources, with high fiber content, because it increases ingestion and decreases retention time (Kuijper et al. 2004). In northern Patagonia, the European hare is considered a competitor of domestic herbivores such as sheep and goats (Bonino et al. 1986; Bonino 1999). Also, the current distribution of this species overlaps with the geographic ranges of native herbivores, such as the mara, *L. maximus* and *Sylvilagus brasiliensis*, and in some cases overlap has been found in the use of trophic resources (Amori and Gippoliti 2003; López-Cortés et al. 2007; Puig et al. 2007).

As medium-sized herbivores, the European hare and the mara have been considered ecological equivalents (Mares and Ojeda 1982; Novillo and Ojeda 2008). Competition for food between these species was also considered one of the causes for the decline in the mara populations (Grigera and Rapoport 1983; Bonino et al. 1997). Since exotic animals can compete with and even displace the native species, and given that these species coexist in Ischigualasto Provincial Park, a hyper-arid ecosystem with scarce food resources, our objective was to evaluate diet composition, relationship between diets and food availability, and trophic relationships of the native mara with the exotic European hare.

We postulate that the mara, like other native herbivores, might overcome difficulties related to scarce resources by an adaptation for choosing resources that are stable over time (Campos et al. 2001a; Sassi et al. 2011). Thus, its diet during the year will be composed of a narrow basic spectrum of plant species, opportunistically incorporating some resources when they appear in high abundance (such as *Prosopis* fruits). On the other hand, the European hare, as an exotic species extending its geographic distribution to the north and arriving in this hyper-arid region only a short time ago, has a diet less fitted to the environment. Then, the European hare's diet will be more diverse and composed of species not available all year long. Nevertheless, considering the low food availability during the dry season, we expect high trophic overlap between both species.

## Materials and methods

### Study area

The study was carried out in Ischigualasto Provincial Park (30° 05′S–67° 55′W) in San Juan Province, Argentina. The Park extends over 62,916 ha at a mean altitude of

1,300 m.a.s.l., and it is included in the northern Monte of hills and close basins ("sierras y bolsones"; Burkart et al. 1999). The climate is arid, with an average annual precipitation of 183 mm. It is characterized by humid summers (average precipitation 100 mm, November–March) and dry winters (average precipitation 8 mm, April–October). Mean temperature in summer is 24.3 °C, with an absolute maximum temperature of 45 °C. Mean temperature in winter is 8.5 °C, with an absolute minimum of −10 °C (De Fina et al. 1962). The landscape is characterized by open scrubland dominated by shrubs (*Larrea cuneifolia*, *Zuccagnia punctata*, *Prosopis torquata*), cacti (*Trichocereus terschesckii*), and bromeliads such as *Deutherocohnia longipetala*, and *Tillandsia* spp. (Márquez et al. 2005; Acebes et al. 2010).

Collection of feces and vegetation sampling were made in the Mesquite woodland community, described by Acebes et al. (2010), which is the habitat most used by mara in the Ischigualasto Park (Beninato 2010). The presence of mara and European hare was confirmed from tracks, fresh feces, and cuts in plants.

Availability of food resources

The supply of plant species was recorded during the dry season (April–October 2005) and the wet season (November–March 2006), considering vegetation cover as an estimation of food availability. Plots were randomly selected across the study area (eight in the wet season and 10 in the dry season), separated by at least 30 m. We established two 25-m perpendicular lines at each plot, and on them we visually estimated plant cover in 13–2 m$^2$ quadrats, through the projection of the exposed leaf area on the ground. The first quadrat was located at the intersection of the lines and the others on the lines 2 m apart, giving a total sampling area of 52 m$^2$ per plot.

Botanical composition of diets

Samples of fresh feces were collected from the Mesquite community in order to estimate the use of food resources. Fecal samples consisted of pellets from different depositions located at least 20 m apart. We were able to identify feces of both herbivores through characteristics of shape and size. Collected samples (mara—wet season $N=15$, dry season $N=11$; European hare—wet season $N=16$, dry season $N=13$) were processed in the Laboratory of the Institute and Museum of Natural Sciences (National University of San Juan). Diet composition was analyzed by microhistological analysis of feces following the method described in Dacar and Giannoni (2001).

For preparing fecal samples for analysis, we used a macerating solution of 17.5 % NaHCO$_3$ (sodium bicarbonate) for about 24 h. The material was rinsed with tap water and

sieved through a metal screen with openings of 74 μm. Three microscope slides were prepared from each sample. Fifty microscope fields were systematically examined on each slide under a microscope at ×400, totaling 150 fields per sample. Histological features of leaf epidermis, seed coats, and fruits were used to identify food items on the slides by comparison with a reference collection, which consisted of microhistological slides of plant material. Only one identifiable fragment, the largest one present, was considered per microscope field. We recorded the presence of a food item and determined its relative percentage of occurrence by dividing the number of fields containing the item by the total number of observed fields (Holecheck et al. 1982).

The potential bias associated with the microhistological analysis of feces as an estimate of herbivore diet composition has been discussed (e.g., Vavra and Holechek 1980; Holecheck et al. 1982). Differential digestibility may cause overestimation of shrubs and grasses in the diet and underestimation of the readily digested forbs. However, when compared to other methods for studying diet composition, the microhistological analysis of feces provided similar results, and it is the least invasive and most practical technique for evaluating dietary composition under field conditions (Mohammad et al. 1995).

Data analysis

Plant species were classified into functional groups as follows: trees, shrubs, annual forbs, grasses, cactaceae, and epiphytes. We used Kruskal–Wallis ANOVA and a posteriori test ($p<0.05$; InfoStat 2008) in order to perform all the comparisons based on functional groups. Thus, we compared among functional groups, for each season, data on food availability and data on herbivore diet.

Diet selection was assessed for plant species with a percent occurrence in diets equal to or of more than 1 %, using Bonferroni simultaneous confidence intervals (Neu et al. 1974; Byers et al. 1984). These intervals determine the actual proportion of use for each plant species and compare it to the expected proportion (Pe=relative plant cover in the field). Plant use was classified as selected, indifferent, or avoided, depending on whether the expected proportion was located below, within, or above the confidence interval of the dietary frequency.

A redundancy analysis (RDA) was applied to the matrix of plant species abundance in the diets, including only species that appeared in at least five samples. This constrained ordination was performed because data sets had a short gradient ($L=2.69$) indicating linear response curves, and explanatory variables were in the form of categorical predictors (Ter Braak and Smilauer 2002). The association of each herbivore (mara and European hare) with each

season (wet and dry) was used as a nominal explanatory variable. Conditional effects of explanatory data on diet data were assessed using Monte Carlo permutation test (199 randomizations). Results of the multivariate analysis were visualized in the form of a biplot ordination diagram and the percentage of the explained variability was used as a measure of explanatory power. Analysis was carried out using RStudio statistical software version 0.95.265 (Free Software Foundation, Inc. 2009–2011; http://www.rstudio.org/).

The Shannon–Weaver index of ecological diversity (Colwell and Futuyma 1971) was estimated as an indicator of trophic niche breadth, that is, a measure of diversity of plant species and their abundance in the diet ($H'=-\sum pj \log pj$ where $pj=nj/N$ is the proportion of the total number of plants of the species $j$, $nj=$number of plants of the species $j$, and $N=$total number of plants). A $t$ test was used to determine whether there were significant differences between herbivores and seasons.

Dietary overlap of all identified items was estimated with Pianka's index (Pianka 1986): $O=(\sum pij\, pik)/\sum pij2 \sum pkj2)1/2$, where $O$ is the degree of overlap between the species $j$ and $k$, and $pij$ and $pik$ are the proportions of the resource $i$ used by the species $j$ and $k$, respectively. Overlap was calculated separately per season. Overlap values range between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap.

## Results

### Availability of food resources

Mean total plant cover in the Mesquite community was 21.65 % during the wet season (25 plant species) and 21.06 % in the dry season (19 plant species). Both seasons showed significant differences in plant cover among functional groups (Kruskal–Wallis, wet season, $H=23.54$, $p=0.0001$, $df=5$; dry season, $H=30.79$, $p=0.0001$, $df=5$), with shrubs being the most abundant cover type (Fig. 1). The most representative species were the shrubs *L. cuneifolia*, *P. torquata*, *Lycium* sp., *Atriplex* sp., and *Bulnesia retama*. The cover of trees was low and the other functional groups did not exceed 1 % (Fig. 1).

### Botanical composition of diets

The items identified in diets were mainly leaves, and fruits only of *Lycium* and *Prosopis* were found. The composition of the mara's diet based on functional groups was significantly different in both seasons (wet season, $H=56.27$, $p=0.0001$, $df=5$; dry season, $H=49.26$, $p=0.0001$, $df=5$). In the wet season, shrubs were the most consumed group, followed by grasses and annual forbs. During the dry season, shrubs were as important as cacti and together represented more than 90 % of the diet (Fig. 1). The diet was composed of 33 plant species

**Fig. 1** Comparison between food availability (*A*; cover of plant species) and diets (relative percentage of occurrence) of European hare (*H*; *Lepus europaeus*) and mara (*M*; *Dolichotis patagonum*) in the wet and dry seasons taking into account plant functional groups. The *point* in the box indicates the median value of the data. The upper and lower hinges of the box indicate the 75th and the 25th percentiles of the data set, respectively. The ends of the *vertical lines* indicate the minimum and maximum data values; the *points* outside the ends of the whiskers are outliers
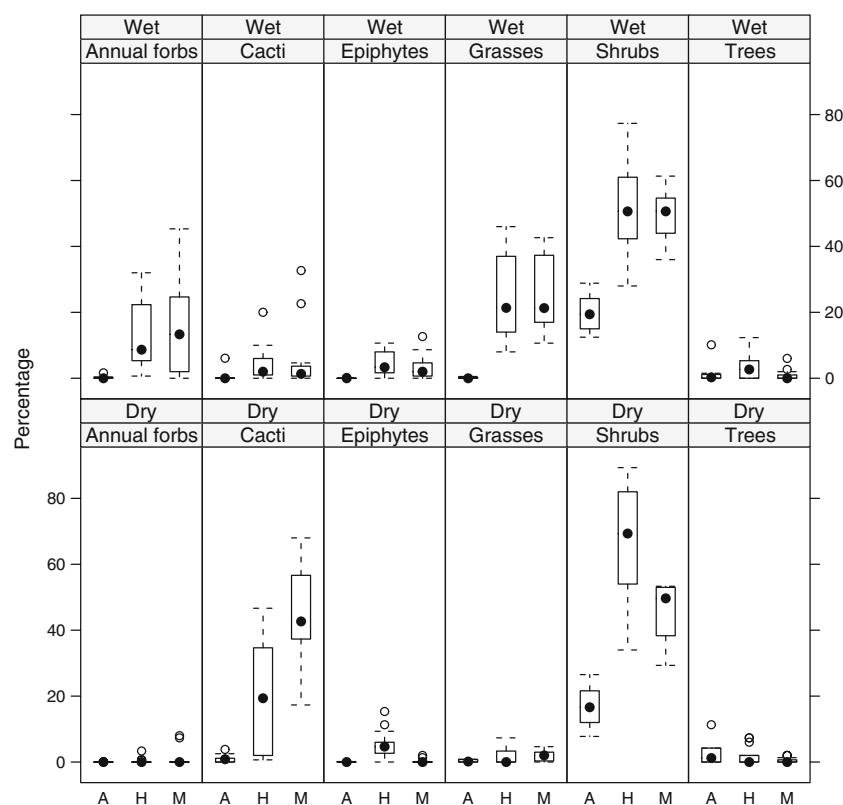
in the wet season and 15 in the dry season. In the wet season, the most representative species among those selected by maras were shrubs such as *P. torquata* and *Atriplex* sp., the grass *Trichloris crinita*, and the annual forb *Tribulus* sp. During the dry season, the mara's diet was composed of similar proportions of the same shrub species, but also contained a higher proportion of cacti such as *Tephrocactus* sp. and *Opuntia* sp. (Tables 1 and 2).

The European hare's diet was composed of 31 plant species in the wet season and 21 in the dry season. Similar to the mara's diet, the main functional groups composing the European hare's diet changed in both seasons (wet season, $H=64.10$, $p=0.0001$, $df=5$; dry season, $H=49.74$, $p=0.0001$, $df=5$). Shrub consumption was high all year round, even increasing in the dry season (Fig. 1). Grasses and annual forbs were the second most representative

**Table 1** Composition of diets (mean of relative percentage of occurrence of plant species±SE) of mara (*Dolichotis patagonum*) and European hare (*Lepus europaeus*) during the wet and the dry seasons in the Ischigualasto Provincial Park (San Juan, Argentina)

| Plant species | Acr | Mara | | European hare | |
|---|---|---|---|---|---|
| | | Wet season $n=15$ | Dry season $n=11$ | Wet season $n=16$ | Dry season $n=13$ |
| *Prosopis flexuosa* | pflex | 0.22±0.14 | 0.54±0.25 | – | – |
| *Geoffroea decorticans* | geof | 0.62±0.38 | – | 3.31±0.91 | 1.91±0.81 |
| Total trees | | 0.84 | 0.54 | 3.31 | 1.91 |
| *Artiplex* sp. | atrx | 9.89±1.80 | 14.21±1.67 | 6.58±1.18 | 21.33±4.17 |
| *Bulnesia retama* | bul | – | 0.12±0.12 | 1.33±0.52 | 19.28±2.40 |
| *Cyclolepis genistoides* | cyclo | 0.35±0.13 | – | 19.58±3.92 | – |
| *Larrea* sp. | | 1.29±0.58 | 0.06±0.06 | 0.46±0.29 | 1.13±0.91 |
| *Lycium* sp. | lyc | 2.75±0.33 | – | 4.45±0.77 | 1.59±0.81 |
| *Lycium* (fruit) | lycfuit | 0.18±0.14 | – | 0.08±0.06 | – |
| *Prosopis* (fruit) | pfruit | 6.68±1.36 | – | 8.45±1.35 | 0.26±0.16 |
| *Prosopis torquata* | ptorq | 25.06±2.83 | 26.48±2.41 | 8.75±2.95 | 7.28±2.04 |
| *Senna aphila* | senn | 0.09±0.06 | – | 0.12±0.07 | 2.20±0.75 |
| *Zuccagnia punctata* | zuc | 0.40±0.24 | 3.94±0.76 | 0.29±0.22 | 0.87±0.36 |
| Total shrubs | | 46.69 | 44.81 | 50.30 | 53.94 |
| *Tribulus* sp. | trib | 10.26±2.42 | – | 9.66±2.11 | 0.15±0.08 |
| *Salvia guilliesii* | salv | 1.09±0.45 | – | 0.79±0.34 | 0.20±0.20 |
| *Solanum eleagnifolium* | | 2.93±1.70 | 1.39±0.94 | 1.12±0.55 | – |
| Total annual forbs | | 14.28 | 1.39 | 11.57 | 0.35 |
| *Aristida* sp. | aris | 3.69±0.94 | 0.18±0.13 | 3.91±1.07 | 0.31±0.21 |
| *Cottea pappaphoroides* | cott | 0.49±0.92 | – | 6.21±1.87 | – |
| *Distichilis spicata* | dist | 0.89±0.37 | – | 1.25±0.43 | – |
| *Pappophorum* sp. | papp | 3.06±0.54 | 0.54±0.28 | 1.00±0.33 | 0.31±0.18 |
| *Sporobolus rigens* | spor | – | – | 3.37±1.47 | 0.05±0.05 |
| *Trichloris crinita* | trichl | 12.53±1.49 | 0.54±0.25 | 6.75±1.28 | – |
| Undetermined grasses | grasses | 3.20±0.55 | 0.66±0.22 | 1.50±0.30 | 0.15±0.11 |
| Total grasses | | 23.86 | 1.92 | 23.99 | 0.82 |
| *Trichocereus terscheskii* | tricho | 0.04±0.04 | 1.45±0.30 | 0.62±0.21 | 3.69±0.90 |
| *Tephrocactus* sp. | tephro | 4.35±2.10 | 34.48±4.22 | 3.50±1.20 | 15.18±3.96 |
| *Opuntia* sp. | opun | 0.75±0.39 | 9.39±0.88 | 0.13±0.07 | 1.02±0.40 |
| Total cactaceae | | 5.14 | 45.32 | 4.25 | 19.89 |
| *Tillandsia* sp. | | 3.24±0.94 | 0.30±0.21 | 4.46±0.87 | 5.38±1.21 |
| Total epiphyte | | 3.24 | 0.30 | 4.46 | 5.38 |
| Undetermined dicot | | – | 2.60±0.30 | 2.58±0.68 | 1.84±0.26 |
| Shannon diversity ($H'$) | | 2.14 | 1.62 | 2.27 | 1.93 |

Only plant species with percentages ≥1 % were included; *n* is the number of fecal samples. The acronym (Acr) of the species used in redundancy analysis (RDA) is mentioned

**Table 2** Plant species selected (S), avoided (A), or used indifferently (I) by mara (*Dolichotis patagonum*) and European hare (*Lepus europaeus*) during the wet and dry seasons in the Ischigualasto Provincial Park (San Juan, Argentina)

| Plant species | Wet season | | | | | Dry season | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Pe | Bonferroni confidence intervals | | | | Pe | Bonferroni confidence intervals | | | |
| | | Mara | | European hare | | | Mara | | European hare | |
| **Trees** | | | | | | | | | | |
| *Geoffroea decorticans* | | | | | | 0.0189 | | | (0.00784–0.03255) | I |
| **Shrubs** | | | | | | | | | | |
| *Artiplex* sp. | 0.0689 | (0.07700–0.12579) | S | (0.04749–0.08810) | I | 0.0408 | (0.12113–0.19146) | S | (0.18906–0.26253) | S |
| *Bulnesia retama* | 0.0616 | | | (0.00431–0.02308) | A | 0.0505 | (−0.00222–0.00502) | A | (0.16869–0.23950) | S |
| *Cyclolepis genistoides* | 0.0000 | (0.00133–0.00793) | S | (0.16948–0.23431) | S | | | | | |
| *Larrea* sp. | 0.5360 | (0.00339–0.02120) | A | (0.02990–0.06409) | A | 0.5900 | (−0.00186–0.00326) | A | (0.00237–0.02142) | A |
| *Lycium* sp. | 0.0653 | (0.00650–0.02679) | A | (0.02944–0.06315) | A | 0.0174 | | | (0.00555–0.02784) | I |
| *Prosopis torquata* | 0.0773 | (0.22353–0.29406) | S | (0.06441–0.10998) | I | 0.0517 | (0.24243–0.32996) | S | (0.05357–0.10042) | S |
| *Senna aphila* | 0.0157 | (−0.00148–0.00308) | A | (−0.00159–0.00399) | A | 0.0521 | | | (0.01004–0.03655) | A |
| *Zuccagnia punctata* | | | | | | 0.0000 | (0.02547–0.06592) | S | (0.00075–0.01744) | S |
| **Annual forbs** | | | | | | | | | | |
| *Tribulus* sp. | 0.0076 | (0.07442–0.12236) | S | (0.07541–0.12378) | S | | | | | |
| *Salvia guilliesii* | 0.0003 | (0.00220–0.01859) | S | (0.00086–0.01533) | S | | | | | |
| *Solanum eleagnifolium* | 0.0000 | (0.01466–0.04133) | S | (0.00288–0.02011) | S | 0.0000 | (−0.00071–0.01631) | I | | |
| **Grasses** | | | | | | | | | | |
| *Aristida* sp. | 0.0020 | (0.02038–0.05021) | S | (0.02441–0.05618) | S | 0.0050 | (−0.00233–0.00653) | I | (−0.00117–0.00816) | I |
| *Cottea pappaphoroides* | 0.0000 | | | (0.04423–0.08376) | S | | | | | |
| *Distichilis spicata* | 0.0000 | (0.04423–0.08376) | S | (0.00346–0.02133) | S | | | | | |
| *Pappophorum* sp. | 0.0030 | (0.01567–0.04292) | S | (0.00208–0.01831) | I | | | | | |
| *Sporobolus rigens* | 0.0000 | | | (0.01999–0.04960) | S | | | | | |
| *Trichloris crinita* | 0.0000 | (0.09410–0.14669) | S | (0.04904–0.09015) | S | 0.0018 | (−0.00159–0.01299) | I | (0.00048–0.01671) | I |
| **Cactaceae** | | | | | | | | | | |
| *Trichocereus terscheskii* | | | | | | 0.0000 | (0.00274–0.02565) | S | (0.02088–0.05431) | S |
| *Tephrocactus* sp. | 0.0309 | (0.05397–0.09662) | S | (0.02095–0.05104) | I | 0.0440 | (0.30449–0.39690) | S | (0.12843—0.19296) | S |
| *Opuntia* sp. | | | | | | 0.0000 | (0.07671–0.13648) | S | (0.00171–0.01988) | S |
| **Epiphyte** | | | | | | | | | | |
| *Tillandsia* sp. | 0.0016 | (0.01699–0.04500) | S | (0.00733–0.02886) | S | 0.0010 | (−0.00221–0.00921) | I | (0.03654–0.07725) | S |

Data in parentheses are Bonferroni confidence intervals; Pe is the expected proportion (relative plant cover in the field). Only plant species with percentages ≥1 % were included

functional groups in the wet season, whereas cacti were more consumed during the dry season (Fig. 1). In the wet season, the major species selected were shrubs such as *Cyclolepis genistoides*, grasses such as *T. crinita* and *Cottea pappophoroides*, and annual forbs such as *Tribulus* sp. During the dry season, the European hare's diet primarily included the shrubs *Atriplex* sp. and *B. retama*, and the proportion of *Tephrocactus* sp. increased.

Regarding the comparisons between diets of the mara and the European hare, the RDA of diet data showed correlation between diet and the explanatory variable [$R^2 = 0.47$, $F(3) = 15.40$, $p = 0.001$] for the first three axes. The first, second, and third axes explained 25.4 %, 16.5 %, and 5.6 % of the total variability, respectively (Fig. 2). Throughout the year,

both herbivore diets were strongly related to shrubs, but the most representative species in each diet were different: the mara was more closely related to *P. torquata* and *P. flexuosa*, and the European hare to *C. genistoides* and *B. retama*. However, *Atriplex* sp. was important in both diets. During the wet season, both herbivores shared the consumption of grasses and annual forbs, such as *T. crinita*, *C. pappaphoroides*, *Aristida* sp., and *Tribulus* sp., and fruits of *Prosopis*. The cactus species *Tephrocactus* sp. and *Opuntia* sp. were shared by both herbivores in the dry season, but they were more closely related to the mara, whereas *T. terscheskii* was consumed mainly by the European hare (Fig. 2).

Dietary diversity differed between seasons for both herbivores (mara, $t = 5.92$, $p = 0.0001$; European hare, $t = 3.83$,

$p=0.0007$). Both diets were more diverse during the wet season (Shannon index value; mara $H'=2.14$, European hare $H'=2.27$), but with a similar diversity index ($t=0.28$, $p=0.7802$). Diets during the dry season were less diverse but, comparing between species, that of the European hare was more diverse (mara $H'=1.62$; European hare $H'=1.93$, $t=3.14$, $p=0.0048$). The diets of the mara and the European hare showed low overlap during the wet season ($O=0.18$), but overlap increased over the dry season ($O=0.63$).

## Discussion

The mara and the European hare are likely close ecological equivalents in terms of dietary similarity. An increase in diet overlap at a time of limited food availability is expected to enhance the potential for strong competition for food resources and could ultimately lead to the exclusion of one species (Wiens 1993). They showed a similar dietary ecology: shrubs were the main food items along the year, and both species expanded their trophic niches during the wet season. In the dry season, they highly overlapped their diets (over 60 %).

Even though the environmental availability of food resources (i.e., plant cover) in the Mesquite woodland community was similar throughout the year, annual forbs and seasonal grasses appeared in the study area during the wet season. Probably, they did not represent a quantitatively important and statistically significant contribution to plant cover but constituted a high quality resource. Maybe for this reason both herbivores increased the breadth of their trophic niche during this season, and narrowed it over the dry season, when the main supplement to shrubs was cacti. Nevertheless, the European hare always presented the most diverse diet.

According to the results, the mara's diet was more specialized than that of the European hare. Only three food items covered 50–60 % of the mara's diet (*P. torquata*, *T. crinita*, and *Tribulus* sp.) in the wet season and two items (*P. torquata* and *Tephrocactus* sp.) in the dry season. In the case of the European hare's diet, 50–60 % was made up of six food items (*C. genistoides*, *Tribulus* sp., *P. torquata*, *T. crinita*, *C. pappaphoroides*, and fruits of *Prosopis* spp.) in the wet season and four items (*Atriplex* spp., *B. retama*, *P. torquata*, and *Tephrocactus* sp.) in the dry season.
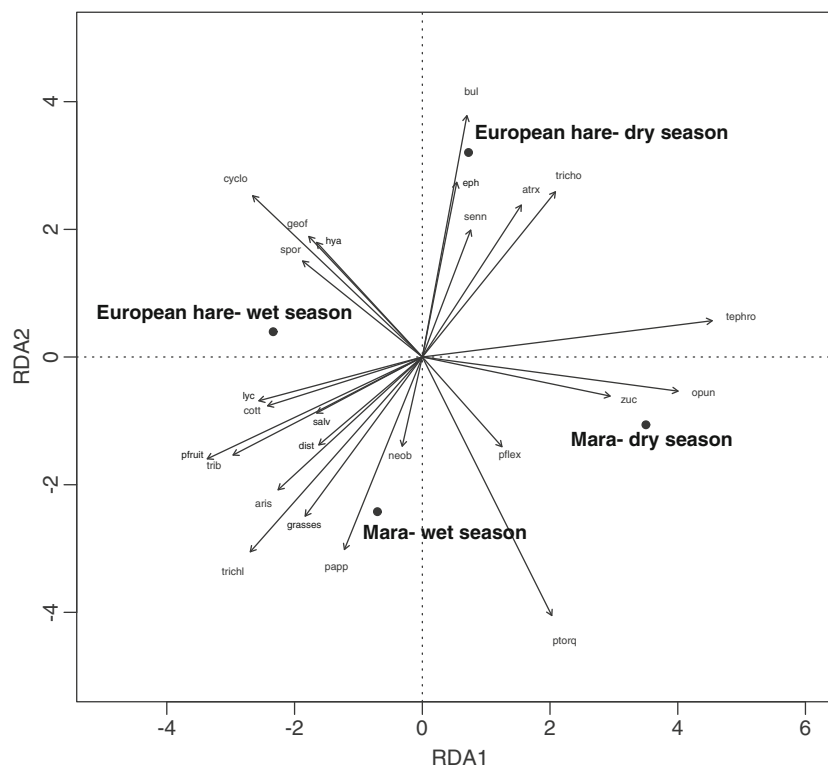


**Fig. 2** Redundancy analysis (RDA) biplot of plant species in the diet and explanatory parameters (herbivores—hare and mara, and seasons—wet and dry). Only plant species that appeared in at least five samples were included. For abbreviations of plant species see Table 1, except *hya* (*Hyalis argentea*), *eph* (*Ephedra* sp.), *neob* (*Neoboutelowa* sp.), and *trib* (*Tribulus* sp.). In the biplot, plant species in the diets are represented by *arrows* and explanatory parameters are indicated by *points*. *Arrows* pointing towards an explanatory parameter point indicate a high positive correlation, *arrows* pointing in an opposite direction indicate a high negative correlation, and *arrows* pointing at a right angle from a line connecting the environmental variable point with the center indicate a near-zero correlation. Species with longer *arrows* and environmental variable points further from the center are more important in the analysis

The mara was classified as a grazer or mixed feeder, with adaptive and opportunistic feeding behavior, and physiologically flexible to tolerate secondary plant compounds (Puig et al. 2010). Mostly in arid environments with strong climate shifts and frequent drought periods, herbivores need to develop responses for coping with food shortage, such as flexible and opportunistic foraging strategies, migratory movements, creation of food-storing sites, and reduction of energy demands (Scoones 1995; Van Horne et al. 1998; Rosi et al. 2003; Gutman et al. 2006).

In the hyper-arid ecosystem of Ischigualasto Park, the mara behaved as an opportunistic mixed feeder because it selected a basic amount of shrubs along the year (almost 50 % of the diet) and supplemented it with annual forbs and grasses in the wet season and cacti during the dry season. These results were interesting because in other ecosystems, even in cases when shrubs were the most abundant food resource available, the mara foraged heavily on grasses (70 % of the diet) (e.g., in the MaB Ñacuñán Reserve—Kufner et al. 1992; Campos et al. 2001b; Schröder 2004; in Las Quijadas National Park—Sombra and Mangione 2005; in Río Negro Province—Bonino et al. 1997; in La Pampa Province—Rodríguez and Dacar 2008; in Patagonia—Puig et al. 2010; in the dry Chaco Phytogeographic Province—Chillo et al. 2010). Nevertheless, the present results are consistent with some studies that found more shrubs and forbs than grasses in the mara's diet (Kufner and Pelliza de Sbriller 1987; Bonino et al. 1997).

Cactus consumption by the mara was reported in previous studies, and it was assumed that this herbivore consumes cacti as a source of water all year round (Sombra and Mangione 2005). In Ischigualasto, the mara's diet was composed of 45.32 % of cacti, such as *Tephrocactus* sp. These species grow in the form of small islands where we recorded feces and the herbivorous activity of maras (personal observation). Regarding diet diversity, the mara's diet was more diverse in the wet than in the dry season, in contrast to findings for the dry Chaco (Chillo et al. 2010) and Central Monte (Kufner et al. 1992).

The same trophic strategy, but selecting different species, was followed by the European hare, whose diet was composed of a basis of shrubs, together with annual forbs and grasses in the wet season, and cacti in the dry season. Similar to the mara, the European hare showed the broadest trophic niche in the wet season, as reported by Bonino et al. (1986) in Patagonia. Nevertheless, studies carried out in the original distribution range of the species (Reichlin et al. 2006 and references therein) and previous studies performed in invaded areas of Argentina, such as Patagonia (Bonino et al. 1986; Pelliza Sbriller et al. 1997; Bonino and Pelliza Sbriller 2006), grasslands of San Luis Province (Giulietti and Jackson 1986), Chaco (Kufner et al. 2008), La Payunia Reserve (Puig et al. 2007), Ñacuñán Reserve (Campos et al.

2001a), and La Rioja Province (Rosati et al. 2000), found that grasses were the main item in the European hare's diet, and that trophic diversity increased in the season when forage availability was low because the European hare supplemented its diets with extra food (Bonino et al. 1986). Even though the European hare showed a lower incorporation of cacti in its diet in comparison to the mara during the dry season, the dietary plasticity exhibited by the exotic species through its consumption of high amount of shrubs in the hyper-arid Monte desert is an interesting result of the present study. Also in the southernmost part of the Monte, Bonino et al. (1997) found a high dietary similarity between European hares and maras, with both diets primarily based on shrub consumption.

Important dietary overlaps were found between the European hare and other native (*Lagidium viscacia* and *L. maximus*) and domestic herbivores (such as goats, horses, and sheep) in Patagonia grasslands where they coexist (Bonino et al. 1986; Bonino 1999; Puig et al. 2007, 2010). However, according to De Boer and Prins (1990), competition between two animal species is only possible when they overlap in habitat and food use and when food supply is limiting. Hence, diet overlap is not sufficient evidence of competition because animals could obtain food resources from different areas depending on movement capability (Prins 2000). On the other hand, it is difficult to establish when a food supply is limiting (De Boer and Prins 1990) because in arid lands this could be the normal condition and animals would be adapted to it. Possibly, in arid environments, limitation in availability of plant resources is more related to quality than quantity of food. For this reason, it is necessary to improve the measurement of food resources available to herbivores in arid ecosystems.

In conclusion, both herbivores used similar food resources and they showed strong dietary overlap across the dry season. They were able to incorporate a great amount of shrubs, showing higher dietary plasticity than in other ecosystems, where they selected mostly grasses. Both species behaved like opportunists by consuming seasonally available items (such as annual forbs, grasses, and *Prosopis* fruits in the wet season). The mara was able to consume high proportions of cacti when food resources were scarce. Thus, we can assume the existence of a potential trophic competition between the mara and the European hare, especially during the dry season when food resources are scarce. These results can be important for the management of drylands in South America, where populations of threatened herbivorous species, such as the mara, coexist with exotic animals, sharing spatial and trophic resources even in protected areas.

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