

Obsessed with grasses? The case of mara *Dolichotis patagonum* (Caviidae: Rodentia)

¿Obsesionada con gramíneas? El caso del mara *Dolichotis patagonum* (Caviidae: Rodentia)

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ABSTRACT

The diet of mara (*Dolichotis patagonum*, Zimmeraman 1780) within the limits of Sierra de las Quijadas National Park (San Luis, Argentina) is described. Other studies regarding mara's diet showed that mara, feeds on different species of grasses and shrubs. However, there is controversy regarding the proportions of these items in the diet or whether this proportion varies seasonally. Considering mara's body size, anatomical features and physiology, we suggest that mara feeds on grasses in a greater proportion than shrubs and forbs. Moreover, giving that in this region precipitation varies considerably between seasons; it is also expected to find a correlation between the diet of mara and seasons. Fecal pellets of mara were collected during four periods including two dry, and two wet seasons. Relative frequency of each item in scats was determined by microhistological analysis. Results support the hypothesis that mara shows preference for grasses, despite they are less available than shrubs and forbs and that this preference remains constant through seasons regardless of the precipitation regime. The characteristics of mara's diet and the ecological implications of these findings are discussed.

Key words: *Dolichotis patagonum*, diet, grasses, preference, Sierra de las Quijadas.

RESUMEN

En este trabajo se describe la dieta de mara (*Dolichotis patagonum* Zimmeraman 1780) en el Parque Nacional Sierra de las Quijadas (San Luis, Argentina). Los estudios realizados sobre su dieta indican que se alimenta de varias especies de gramíneas y arbustos. Sin embargo, existe cierta controversia acerca de la proporción en que se presentan estos ítemes, y si las mismas varían estacionalmente. En base al tamaño corporal de mara, y a sus características anatómicas y fisiológicas, se propone que mara consume una mayor proporción de gramíneas que de otras hierbas no gramíneas y dicotiledóneas en general. Además, esperamos una variación estacional de la dieta, correlacionada a una posible variación estacional en los recursos alimentarios asociada a las precipitaciones. Se colectaron muestras de heces correspondientes a cuatro estaciones en el parque, dos estaciones secas y dos lluviosas. Mediante análisis microhistológico se determinó la proporción de cada ítem medido como frecuencia de aparición en las heces. Los resultados apoyan la hipótesis de un consumo preferencial de gramíneas por parte de mara. Las gramíneas aparecen en mayor proporción en la dieta a pesar de estar en menor disponibilidad en el hábitat y sin que el régimen de precipitación tenga algún efecto. Se discuten las características de la dieta de mara y las implicancias ecológicas relacionadas con esta especie.

Palabras clave: *Dolichotis patagonum*, dieta, gramíneas, preferencia, Sierra de las Quijadas.

INTRODUCTION

Diet analyses are essential to begin to understand physiological and ecological parameters of the species under study (Chivers & Langer 1994, Castellarini 1998, Cortés et al. 2002). When resource quality and availability is low, physiological capacities and constraints

are evident, showing the limits for extracting and using nutrients and energy (Kenagy et al. 1999).

Small rodents usually have high food intake rates of low nutritional quality diets (i.e., high fiber levels) (Kenagy et al. 1999), therefore they keep a relative constant rate of digestible energy. There is evidence that the use of low

quality diets is lower in rodents below a body mass of 10 kg, due to restrictions imposed by size (i.e., low retention time and higher mass specific metabolic rate) (Cork 1994). What would be then, with the feeding behavior of rodents that feed on low quality diets, and whose body mass are at the limit between small and large body size herbivores?

To evaluate this question we studied the diet and feeding behavior of *Dolichotis patagonum* or mara, a rodent of the Caviidae family, inhabiting the relatively low productivity habitat of the xerophitic flats of central and southern Argentina, with an average body mass of 8 kg (Kufner & Prelliza de Sbriller 1987, Redford & Eisenberg 1992). Maras forage heavily on grasses (Taber 1987, Campos & Ojeda 2001). However, other studies showed that maras feed more forbs and shrubs than grasses (Kufner & Pelliza de Sbriller 1987). Bonino et al. (1997) showed that maras feed on grasses and dicots in the same proportion. At the time, it is impossible to evaluate the trophic behavior of maras, given that none of the studies mentioned above have estimated trophic resource availability for this species.

Precipitations in central Argentina, including our study site, vary considerably with seasons. For this reason, we think that some characteristics of the diet of maras, quality and availability, may fluctuate with rainfall. In addition, given mara's body size, it would not have major problems leading with high fiber diet (grasses) but it may have problems dealing with plant toxins (higher in forbs and shrubs than in grasses), due to low toxin turnover rates (Foley & McArthur 1994). There are no data regarding mara's feeding behavior in relation to food availability, therefore and considering mara's physiological characteristics we hypothesized that mara consumes more grasses than shrubs and forbs, and that grass consumption is higher during the wet season than dry season.

MATERIAL AND METHODS

Study site

Sierra de las Quijadas National Park (32°47' S and 67°10' W at 800 m of altitude) is located 116 km north of San Luis City in Central Argentina. The habitat is an ecotone between the Monte (xerophytic, resinous and thorny

shrubs) and the Chaco (hardwood forests) (Cabrera 1976). This region is one of the driest areas in the province (350 mm annual average). Within the limits of the Park, three different habitats are distinguishable: Potrero de la Aguada, Creosote bush flats and the Sierra habitat dominated by Chaco vegetation (hardwood forests).

Sampling

Fecal pellets of maras were collected from two different areas, Creosote bush flats and woods-thorny shrubs in the Sierra habitat. Fecal pellets presenting white coloration or a crackly texture were considered old and therefore discarded. Mara's scats were collected in four field trips, two dry seasons, September 2000 (Dry 1, n = 11) and August 2002 (Dry 2, n = 29), and two wet seasons April 2001 (Wet 1, n = 14) and December 2002 (Wet 2, n = 20). Feces were collected in paper brown bags. Collecting effort was equal to seven hours/day during three days. Once in the laboratory, samples were frozen (-25 °C) until analyses. A reference database of the plants present in the sampling area was made in order to identify the epidermal fragments of the plants in feces.

Availability

Biomass availability measured as kilograms per hectare of cacti and creosote bush (*Larrea* sp. Cav.), two of the most abundant dicots available for maras in the environment and grasses was evaluated considering all plant material of this species available from the floor up to 0.6 m in two different areas: Creosote bush flats and Sierra habitat (woods-thorny shrubs). The available dry mass of creosote bush was estimated during two different dates, the first one in (10/06/2001) and the second one in (09/18/2003). The first biomass estimation was carried out by performing three transects in a flat area dominated by creosote bush and two transects in the Sierra habitat. Each transect was 200 m long and 2 m wide. The data collected consisted in counting the numbers of branches of *Larrea* sp. contained in 2 m². These data were related to water content of branches of this species. The number of squares per transect were 10. The second biomass estimation was done by performing a single 80 x 2 m transect.

Branches of all plants of *Larrea* sp. within the transect were counted. For dry mass availability estimations, ten branches were randomly cutted from each plant in the latest transect and oven dried until constant mass. This data was used to estimate the average dry mass of branches of *Larrea* sp. and hence the biomass availability for both biomass estimations (years 2001 and 2003). Biomass of grasses were measured in July, October and December in 2001, August and December in 2002, in the same areas described above, using 12 transects of 200 x 1 m. All grass mass was removed from 1m² every 20 m, stored in plastic bags, weighted in the field and oven dried until constant mass in the laboratory. Finally, cacti samples (pads) were collected in 12 transects of 200 x 1 m (same dates of grasses measurements). The number of pads per cacti plant were counted. Plant samples were treated as described previously.

Microhistological analysis

For epidermis identification the protocol proposed by Williams (1969), was followed with modifications. Briefly, from each pool of feces, three to four scats were randomly selected. Twenty milliliters of alcohol/water solution (70:30) were added to 200 mg of ground powder and let it rest for four hours. Later, the supernatant was removed and boiling water was added. The solution was left to rest for 12 hours. By this method epidermis is separated from the mesophile of the leaves and fat is removed. Sodium hypochlorite (50 %) was used to bleach the epidermis. The tissue was later fixed by using diluted safranin (1:1 in ethyl alcohol 96 %).

Plant material was ground with mortar and pestle using liquid nitrogen (Hansson 1970). Samples were boiled 10 min in ethyl alcohol 96 %, and later on sodium hydroxide for another ten minutes. Plant samples were bleached and stained with safranin. To refine the identification of plant material in feces, abaxial and adaxial epidermises were observed from the reference collection if needed. Other structures like, stems, seeds and roots parts were used for identification purposes. These samples were treated by directly bleaching the tissues and removing the epidermis with a razor blade (Hansson 1970). Mounting of the samples was done by adding 0.2 mL of the plant material-safranin

solution in a slide. A drop or two of mounting liquid (phenol, glycerin and jelo) were added.

Identification and quantification of plant samples:

Absence-presence and morphology of macro and micro-hairs, thorns, prickle hairs, papillae, silica bodies, stomata cells, and stomatal guard cells of stomata were taken into account as identification criteria (Metcalf 1960, Hansen 1978, Johnson et al. 1983). There after we will call "grasses" (G) to all Poaceae and "shrubs plus forbs" (SF) to all dicots and one monocot genera '*Tillandsia*' spp. The minimum number of microscope fields observed for calculation of relative frequency (RF) for each plant species in each fecal sample was 40. All plant fragments were identified using 500 to 1,250 x total augmentation. Quantification of relative frequency was done at 1,250 x of total augmentation. Relative frequency (RF) was calculated using:

$$\frac{\text{Number of fields in which a fragment of plant was observed} \times 100}{\text{Number of total fields}}$$

An average of RFs for each plant and season is shown in Table 1.

Statistical analysis

We used Chi-squared (χ^2) for all statistical analyses. First, we compared average G and SF frequencies regardless the effect of seasons. Second we tested for G and SF frequencies across seasons and for each season. Finally, we performed two other tests for G and SF frequencies distribution between wet seasons and dry seasons. When multiple comparisons were needed Bonferroni correction was used (Persons & Uetz 1996, Linde et al. 2004). *P* values lower than 0.05 were considered significant. Bars on Fig. 1 represent one standard deviation.

We used the Ivlev's electivity index to test the preference between the following food categories G and SF considering cacti and cresote bush (two of the most abundant dicots available for maras in the environment) by using the equation:

$$E_i = (r_i - p_i) / (r_i + p_i) \text{ (Morrison et al. 1978)}$$

where the electivity (E) is a function of availability of food types in the environment (p) and their relative use in the diet (r). If r and p are equal ($E = 0$), for a food type then, the animal is choosing it in a direct proportion to its relative availability. If r and p differ, the index ranges from -1 (total avoidance) to $+1$ (total preference).

RESULTS

Diet composition

Maras consume at least 24 different plant items of Grasses and 22 items of shrubs plus forbs Table 1. The most consumed species among grasses for all seasons was *Pappophorum* sp. (Shreber) (see in bold). On the other side, leaves of *Prosopis* sp., DC. and fruits of *Prosopis* (Cavanilles ex Lagasca) DC.

torquata, were the most consumed species among forbs (also in bold). Cacti appeared at an average RF of 11 % for all seasons (see in italics).

Grasses in feces were at higher RFs than shrubs plus forbs, for three of the four seasons considered. On average, for all seasons, G were found at a RF of 70 %, and this value was significantly higher than SF. ($\chi^2 = 7.9$ df = 1 P = 0.004), Fig. 1. Neither differences between seasons ($\chi^2 = 5.88$, df = 3, P = 0.11), nor differences between dry seasons $\chi^2 = 1.37$, df = 1, P = 0.24) and wet seasons $\chi^2 = 2.53$, df = 1, P = 0.11 were detected (both analyses were Bonferroni corrected). More than 50 % of grasses are present in all seasons, but only 30 % of SFs species are present in the seasons considered. Non recognized fragments (NRF), are fragments identified only as grasses or shrubs plus forbs and are shown with a number in Table 1.

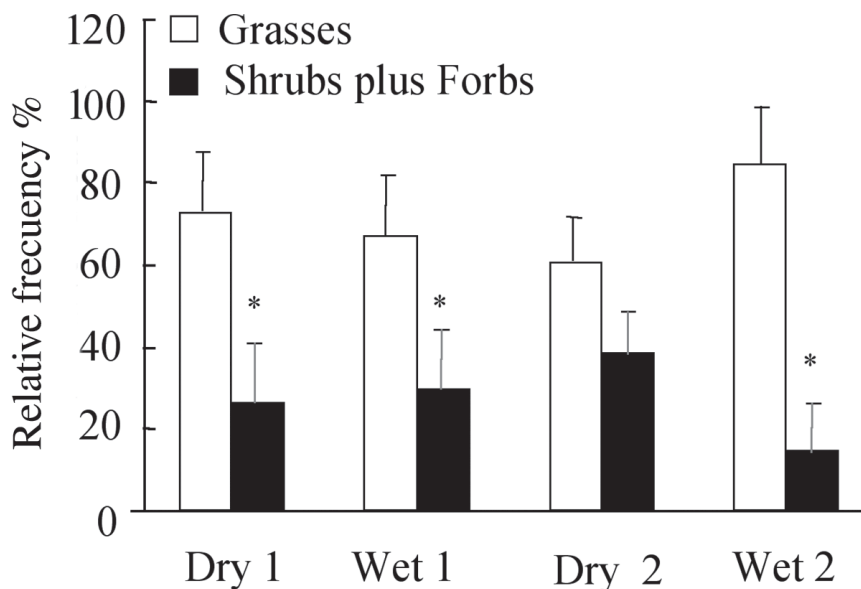


Fig. 1: Relative frequency of grasses and shrubs plus forbs in mara's diet in different season at Sierra de las Quijadas National Park. Asterix indicate statistical differences between grasses and shrubs plus forbs. Chi square χ and P values for G and SF by season were: Dry 1 ($\chi^2 = 8.6$ P = 0.013), Wet 1 ($\chi^2 = 6.40$ P = 0.045), Dry 2 ($\chi^2 = 1.88$ P = 0.67) and Wet 2 ($\chi^2 = 19.42$ P < 0.0001). * P values are Bonferroni adjusted values (times four). Significant values are shown in bold.

Frecuencia relativa de gramíneas y arbustos más herbáceas en la dieta de mara en diferentes estaciones en el Parque Nacional Sierra de las Quijadas. Asteriscos indican diferencias entre gramíneas y arbustos más herbáceas. Los valores de χ^2 para G y SF por estación fueron: Seca 1 ($\chi^2 = 8.6$ P = 0.013), Lluviosa 1 ($\chi^2 = 6.40$ P = 0.045), Seca 2 ($\chi^2 = 1.88$ P = 0.67) y Lluviosa 2 ($\chi^2 = 19.42$ P < 0.0001). * Los valores de P están corregidos por Bonferroni (multiplicado por cuatro). Se muestran en negrita los valores estadísticamente significativos.

TABLE 1

List and relative frequency of plant species in mara's diet across seasons
 Listado y frecuencia relativa de especies de plantas en la dieta de mara en las diferentes estaciones

	Date			
	23/09/2000	08/04/2001	09/08/2002	28/12/2002
Grasses	Dry 1	Wet 1	Dry 2	Wet 2
<i>Aristida</i> sp.	-	2.5	3.1	2.5
<i>A. mendocina</i>	-	5.0	3.8	3.8
<i>A. minutiflora</i>	2.5	2.5	2.5	5.8
<i>Bouteloua</i> sp.	3.8	2.5	3.8	5.7
<i>Cottea pappophoroides</i>	-	-	-	11.4
<i>Chloris</i> sp.	5.0	2.5	3.4	2.5
<i>Digitaria californica</i>	-	3.3	4.2	6.3
<i>Eragrostis</i> sp.	2.5	2.5	3.1	4.7
<i>E. lugens</i>	-	5.0	-	5.0
<i>E. cilianensis</i>	-	3.8	2.5	2.5
<i>Gouinia paraguayensis</i>	5.0	2.5	2.5	4.2
<i>Neobouteloua lophostachya</i>	5.7	6.1	5.5	5.2
<i>Pappophorum</i> sp.	29.8	30.7	30.0	13.8
<i>Setaria</i> sp.	5.0	7.3	3.9	4.7
<i>Sporobolus</i> sp.	8.6	4.1	5.9	9.9
<i>Sporobolus pyramidatus</i>	11.4	5.0	5.4	7.8
<i>Sporobolus</i> (G3)	3.3	5.0	3.3	3.8
<i>Tragus berteronianus</i>	2.5	2.5	2.5	2.5
<i>Trichloris crinita</i>	5.4	6.3	7.0	3.8
Grass 12	7.5	3.1	-	8.3
Grass 9	2.5	-	-	3.3
Grass 19/10	3.8	-	-	2.5
Grass 13	2.5	2.5	-	2.5
NRF (grass)	13.6	10.7	12.2	25.5
Shrubs and forbs				
<i>Prosopis</i> sp.	13.2	5.5	9.6	5.8
<i>Prosopis flexuosa</i>	6.3	4.4	9.4	4.1
<i>Prosopis torquata</i>	2.5	2.5	4.3	-
<i>Prosopis</i> (Fruit)	3.3	8.3	4.2	4.5
<i>Cereus aethiops</i>	7.5	5.0	5.6	2.5
<i>Opuntia sulphurea</i>	3.8	2.5	6.5	10.8
<i>Tillandsia</i> sp.	-	-	2.5	-
Dico 7	2.5	-	-	-
Dico 31	3.0	-	5.0	2.5
Dico 22	-	2.5	3.8	2.5
Dico 9	-	-	-	7.5
Dico 43	9.6	-	7.2	2.5
<i>Atriplex</i> sp.	-	9.8	7.5	7.0
DicoNR1	3.8	2.5	5.3	12.5
<i>Geoffroea decorticans</i>	5.0	6.7	4.0	5.0
<i>Acacia</i> sp.	-	-	-	5.0
Dico 29	-	-	2.5	5.0
Dico 12	-	-	-	2.5
Dico 20	2.5	-	2.5	10.0
<i>Larrea cuneifolia</i> (root)	-	3.0	2.5	-
<i>Larrea cuneifolia</i>	3.3	-	4.6	-
NRF (dicot.)	-	3.3	-	4.3

Resource availability

Analysis of biomass availability at the Park show that SF are greater than G. For wet season we found a mean value of $21.2 \pm 4.5 \text{ kg ha}^{-1}$, $n = 24$ for cacti and, considering all species of grasses, biomass was $6.85 \pm 4.5 \text{ kg ha}^{-1}$, $n = 24$. On the other hand the dry season show, for the two dominant genera of dicots in the study area, mean values of $22.1 \pm 20 \text{ kg ha}^{-1}$, $n = 24$ (cacti) and $434 \pm 180 \text{ kg ha}^{-1}$, $n = 6$ (cresote bush); while grasses biomass was much more low $9.47 \pm 6.6 \text{ kg ha}^{-1}$, $n = 32$. The Ivlev's electivity index shows a positive value for grasses (0.95) and a negative value for shrubs plus forbs category (-0.53).

DISCUSSION

In this study, we considerably advance knowledge regarding the relationships between consumption of plants, precipitation and trophic resource availability. Maras consumed more grasses than shrubs plus forbs regardless trophic resource availability or precipitation in the study area. On average for all seasons, grasses appeared in the diet in a higher proportion compared to shrubs plus forbs (70:30) (Fig. 1) and there was no seasonal variation between these two trophic categories. Biomass availability in the Park showed that SF were at least 70 x fold greater than grasses, $434 \pm 180 \text{ kg ha}^{-1}$ (cresote bush) and $22.1 \pm 20 \text{ kg ha}^{-1}$ (cacti) versus $9.47 \pm 6.6 \text{ kg ha}^{-1}$ of dry mass for grasses. Moreover, maras showed a strong preference for G (0.94) over SF (-0.53) according to the Ivlev's index.

The most consumed grass was *Pappophorum* sp. No relationship between biomass availability of this grass and consumption has been established yet, however it is one of the perennial grasses in the Park. Protein content of *Pappophorum* sp., is similar to the rest of the grasses consumed by maras (about 7 %) (Ávila personal communication). However, the rest of the forbs available for mara are higher in protein 12 % to 16 %, for *Larrea* sp. and *Prosopis* sp. respectively (Ávila personal communication) (Mabry et al. 1977). Cacti appeared at a relative frequency of 11 % in feces through seasons. Besides cacti remnants in feces, mara's bite marks on cacti (*Cerus aethiops* Haw., *Opuntia sulphurea* Gillies ex Salm-

Dyck.) were evident. Given that grasses compose 70 % of mara diets, but that only have 25 % of water, and cacti have 75 % water (Nuñez personal communication) it is thought that mara may consume cacti as a source of water all year around. Another finding is that even though C_4 plants are dominant over C_3 plants in the Park (95 %) and they are the only ones present in mara's diet we have no relationship established between type of plant and its biomass availability. However, is interesting noting that C_4 are high in fiber (cellulose and hemicellulose) and low in plant secondary metabolites.

The inclusion of items high in fiber in the diet of herbivores is considered a challenge because of its relative low digestibility and because fiber limits the ingestion and digestion of other nutrients (Cork 1994). Even though, herbivores have fermentation chambers that facilitates fiber digestion and absorption, the efficiency diminishes with body size reduction. (Batzli & Hume 1994). This is mainly due to the high mass specific metabolic rate and short retention times of small herbivores, reducing microbial fermentation and hence energy extraction (Hume 1989). Herbivores ranging between 20 up to 2.000 g, show different colon or ceacum modifications allowing them to incorporate fiber in their diets. When body size increases, these modifications are not present, this may be related to the higher retention time and a higher total gut capacity than small herbivores (Hume 1989). Mara, with an average body mass of 8 Kg, is the largest of the cavids and the second largest rodent after capybara (*Hydrochaeris hydrochaeris*, L. 1766), should then show no major troubles leading with fiber.

Plant secondary metabolites represent another source of challenge for herbivores, while some of them avoid plant toxins, others can tolerate high doses of these toxins (Foley & McArthur 1994, Dearing et al. 2000 Mangione et al. 2000). A model of factors involved in diet choice by herbivores has been developed by McArthur et al. (1991). Two extreme responses to plant toxins are proposed in the model. On one side there are those who completely avoid PSMs, on the other side, the specialists. The latest are the ones capable of dealing with high doses of single toxins (i.e., koalas). According to this model, mara seems to occupy the niche of those herbivores avoiding plant secondary compounds, even though its diet seems to be high in fiber.

Are mara's preferences of grasses or avoidance of forbs and shrubs related to a low tolerance to plant secondary metabolites? Large body size herbivores, have higher retention and toxin turn over times than smaller ones. Therefore, they may be more exposed to the toxic effects than small herbivores (Foley & McArthur 1994). *Dolichotis patagonum* represents then, an excellent model to test hypothesis regarding the role of body size on tolerance to plant secondary metabolites in herbivores.

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