Original article

# Niche partitioning and coexistence between two mammalian herbivores in the Dry Chaco of Argentina

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## ARTICLE INFO

## ABSTRACT

Competitive interactions are known to be stronger between morphologically similar and phylogenetically closely related sympatric species. Patagonian mara (*Dolichotis patagonum*) and Chacoan cavy (*Pediolagus salinicola*) are two medium-sized herbivorous mammals which have disjunctive distributions within a sympatric region characterized by dry woodlands and shrublands (Dry Chaco, Argentina). The niche partition hypothesis predicts that ecologically similar species living together should show differentiation in at least one of the main niche dimensions to avoid competition. Thus, we predict that Patagonian mara and Chacoan cavies will differentiate in the use of trophic and/or spatial niche. To prove this hypothesis, we sampled 26 study sites in the dry and wet season and collected fresh faeces of both species. We estimated the diet composition using microhistological analysis of faeces. For habitat analysis we measured 16 vegetation variables, as well as habitat complexity and heterogeneity structure. Our results showed that during the dry season, both species segregate their diet but not their habitat niche, whereas during the wet season they segregate their habitat, and diet segregation is diffused. Diet overlap was similar between seasons, indicating a change in the foraging strategy of the cavy, which selected forbs, grasses, succulents and trees in the dry season and only grasses in the wet season. Our results support the niche partition hypothesis as a mechanism of coexistence among ecologically similar species in the South American temperate arid lands.

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## 1. Introduction

Ecological niche theory describes biotic and abiotic resources affecting the fitness of a species or population. Beneath this theory lay two principal descriptors that allow ecologist to relate populations to their surroundings: niche breadth and niche overlap (Hutchinson, 1957). Niche breadth is a quantitative description of the degree of use of a particular resource, and it varies depending on resource availability, competitors and climate fluctuations (Feinsinger et al., 1981). Niche overlap occurs when species use the same resource in similar ways (Colwell and Futuyma, 1971). Theoretically, under the resource-utilization niche concept (Shoener, 2009), two species cannot occupy the same n-dimensional ecological niche without exerting strong competition on each other, since this would result in potential local extinction of one of the species (MacArthur and Levis, 1967). Thus, the niche partition hypothesis predicts that the coexistence of ecologically similar species should show differentiation in at least one of the main niche dimensions in order to avoid competition. Segregation of food, space and/or time is mechanisms which allow the ecological coexistence of species (Schoener, 1974; Pianka, 1981; Jaksic and Marone, 2002).

Competitive interactions are known to be stronger between morphologically similar and phylogenetically closely related sympatric species (Schoener, 1974; Loveridge and Macdonald, 2003; DiBitetti et al., 2009). Studies on sympatric herbivores have shown that high overlap in one niche dimension is accompanied by avoidance in another niche dimension (Luo and Fox, 1996; Wei et al., 2000; Stewart et al., 2002). Moreover, coexisting species are expected to develop strategies for niche differentiation when resources become scarce (MacArthur and Levis, 1967). In arid lands, where rainfall is an unpredictable and markedly seasonal resource, food and habitat are the main limiting factors preventing coexistence of herbivores (Whitford, 2002).

The Patagonian mara (*Dolichotis patagonum*, Zimmerman, 1780) and the Chacoan cavy (*Pediolagus salinicola*, Burmeister, 1876) (Rodentia, Caviidae, Dolichotinae) are closely related phylogenetically,

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and are endemic to the temperate arid and semiarid regions of southern South America. The Patagonian mara inhabits the Monte and Patagonian Deserts of south-central Argentina (Campos et al., 2001b) and prefers open habitats with sparse shrubs (Taber, 1987; Kufner and Chambouleyron, 1991; Baldi, 2007; Rodriguez, 2009). Its diet varies along its geographic distribution, and it has been characterized as a generalist herbivore with a preference for grasses (Kufner and Pelliza de Sbriller, 1987; Bonino et al., 1997; Campos et al., 2001a; Sombra and Mangione, 2005; Rodríguez and Dacar, 2008). The Chacoan cavy inhabits the South American Chaco, from western Paraguay to west-central Argentina (Cabrera and Yepes, 1960). This species is also characterized as a generalist herbivore, but feeds primarily on forbs. It prefers open woodlands and shrublands (Rosati and Bucher, 1995). At a geographical scale, these species show disjunctive distributions, however, there is a particular area of the Dry Chaco where they are sympatric (Olrog and Lucero, 1980; Ojeda, unpubl. data). This region is an ecotone between Chaco and Monte biogeographical regions, characterized by degraded vegetation due to fire, logging and grazing (Karlin et al., 1994; Chillo and Rodriguez, pers. obs.). This situation offers a unique natural opportunity for testing coexistence mechanisms between ecologically similar herbivorous mammals.

According to the niche partition hypothesis, we predict that *P. salinicola* and *D. patagonum* will segregate in the use of at least one of the niche dimensions (trophic and/or habitat) in order to diminish potential competition. Thereby, the objectives of our study where to: 1) characterize and compare the use and selection of food resources between cavies and maras throughout the year; 2) analyze trophic niche breadth and overlap of cavies and maras under different food availability (wet and dry season); and 3) characterize and compare habitat use by these species throughout the year.

## 2. Material and methods

### 2.1. Study area

Our study was carried out in the Bajondo region (31°25′ S; 65°37′ W) in the north-west extreme of Cordoba province (Argentina), were cavies and maras occur sympatrically (Fig. 1). This region is characterized by the Dry Chaco Phytogeographic Province (Cabrera, 1976), a heterogeneous landscape with patches of woodlands, savannas, salt basins and low hill mountains (Karlin et al., 1994). The climate is markedly seasonal, with wet and dry seasons (November to March and April to October respectively), and high water deficit along the year. Average annual rainfall ranges from 400 to 500 mm, and annual mean temperature is 18 °C, with maximums that can exceed 40 °C during summer (Cabrera, 1976).

The region is dominated by open woodlands of *Aspidosperma quebracho-blanco*, *Prosopis chilensis*, *P. flexuosa*, *Cercidium praecox* and *Geoffroea decorticans*. The shrub stratum is composed of *Acacia* sp., *Schinus fasciculatus*, *Senna aphylla*, *Larrea divaricata*, *L. cuneifolia*, *Capparis atamisquea*, *Bulnesia retama*, *Suaeda divaricata,* and *Courtesia cuneifolia*. During the wet season there is also a grass and forb layer dominated by *Chloris vaginata*, *Setaria sp.*, *Solanum argentinum*, *Evolvulus arizonicus*, *Bouteloua aristioides*, *Neobouteloua lophostachya*, *Sporobolus sp.* and *Pappophorum* sp. (Morello, 1958; Karlin et al., 1994).

### 2.2. Species biology

The Chacoan cavy was first assigned to *Dolichotis* genus (Burmeister, 1876), but Marelli (1927) changed the genus to *Pediolagus* due to differences in external and internal characteristics, such as theirs body sizes (mara's head-tail length is 740 mm and cavies are 460 mm) (Yepes, 1935). Actually, both species are the unique
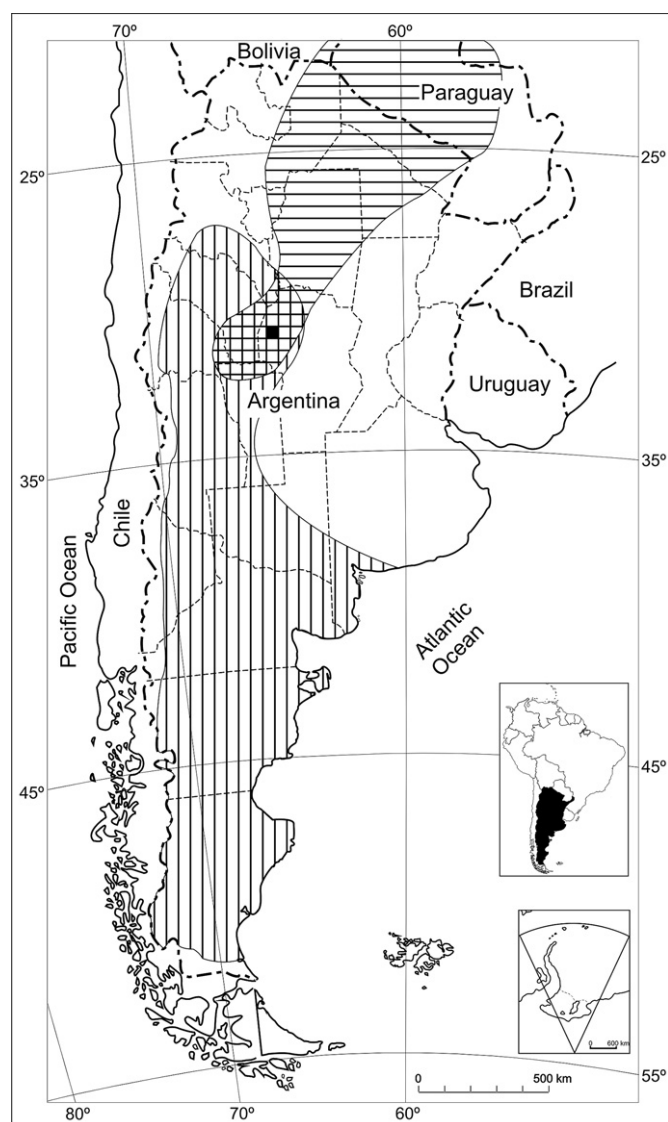


**Fig. 1.** Map distribution of *Dolichotis patagonum* (vertical lines), *Pediolagus salinicola* (horizontal lines) and study site (bold square) in the dry Chaco of Cordoba's Province, Argentina.

members of the Subfamily Dolichotinae (Pocock, 1922). Species also differ in the size and colour of their faeces. Chacoan cavies deposit their fresh faeces in groups of 5.45 faeces (SD = 2.81), with a mean length of 15.17 mm (SD = 2.197) and a mean wide of 5.83 (SD = 0.628) (Chillo, pers. obs). They are dark green, with sharp extremes, and some of them present a central groove. Patagonian mara's fresh faeces are light green to brown in colour, with rounded extremes, and a curved shape with a central groove on the concave side. Pellets are composed by a mean of 7.79 faeces (SD = 0.752), and each faeces shows a mean length of 23.15 mm (SD = 1.28) and a mean width of 7.09 mm (SD = 0.219) (Rodriguez, pers. obs.).

Chacoan cavies are mainly diurnal and live in family groups (Wilson and Kleiman, 1974). Patagonian maras are also diurnal and theirs social organization combines monogamy and communal denning (Taber, 1987). Each couple has its own territory during the non-breeding period, but they overlap for communal breeding (Taber, 1987; Redford and Eisenberg, 1992). Due to the social behaviour of both species, faeces cannot be assigned to individuals, but to territories (Rosati and Bucher, 1995; Rodriguez, 2009).

### 2.3. Sampling design

Inside the Bajondo region we selected 13 sample sites in late winter of 2006 (dry season) and 13 sample sites in middle summer of 2008 (wet season). There was neither fire nor drought, and cattle management remained stable between sampling periods. Sampling sites were at least 300 m apart from each other.

Habitat use is defined as the area use by a species or a population, indicated by indirect evidence, like faeces, footprints or burrows, or direct observation of the individuals (Rosati and Bucher, 1995; Rodriguez, 2009). As individuals of maras and cavies can only be differentiated with capture-mark techniques, we analyzed the habitat used by the entire population, not by the individual. At each sample site we recorded the presence or absence of signs or individual for both species. We quantified habitat use for each species measuring habitat structure and composition of vegetation by using the modified Point Quadrat method (Passera et al., 1986). We placed a 30 m long line transect with 100 sample stations at each sample site ($n = 26$). At each sampling station we recorded the vertical distribution of plants by noting every species present at 25 cm intervals from the soil level to 2 m high, resulting in a total of 9 vertical layers.

For diet analysis, we searched and collected fresh faeces of maras and cavies along a $50 \times 10$ m band transect (500 m$^2$ areas) at each sample site. Transects were perpendicular to vegetation transects. All pellets where assigned to the right species but as they could not be assigned to individuals, all pellets from each specie found in each band transect where pooled together in order to include the variability in diet of each site (Rosati and Bucher, 1995). Available resources were estimated using the percent cover of each plant species up to 1 m tall, obtained by Point Quadrat sampling, because neither species can feed at higher levels.

### 2.4. Data analysis

We used the microhistological technique for analyzing faecal contents (Dacar and Giannoni, 2001). Five microhistological slides were prepared for each sample and 50 microscopic fields were systematically examined for every slide using $40\times$ magnifications, identifying the biggest item in each microscopic field. Plant items (epidermal tissue only) were identified using plant reference material from the study site. Relative frequency of occurrence of the different plant species in faecal samples was estimated by dividing the number of fields containing one species by the total number of fields (Holechek and Gross, 1982). The Shannon Diversity Index (H′) was used to estimate diet diversity. The U Mann–Whitney non parametric test was used to compare each item consumption (as plant life form: trees, shrubs, forbs, grasses and succulent) between Chacoan cavy and Patagonian mara (Zar, 1999).

To assess resource selection we calculated the Preference Index (PI) (Krueger, 1972) and it's Standard Error (SE) (Hobbs and Bowden, 1982). Resources are selected if the PI $\pm$ t($\alpha$/freedom degrees) $\times$ SE confidence interval falls entirely above 1; not selected when this confidence interval falls entirely below 1; and used proportionately to their availability when the confidence interval includes 1.

Niche breadth was calculated using the Standardized Niche Breadth Index (B$_A$) proposed by Hulbert (1978). To analyze niche overlap between species we used the Similarity Proportion Index (PS) (Colwell and Futuyma, 1971). This index ranges from 0 to 1, the highest number representing maximum overlap in the use of available resources.

In order to quantify habitat use we recorded habitat characteristics from the vegetation samples, for each sampling site where mara or cavy signs were present. Sixteen habitat variables were quantified: cover of bare soil, litter, grasses, forbs, succulents, shrubs, trees, and 9 vertical layers separated by 25 cm. Differences were analyzed using a t test. Heterogeneity (horizontal structure) and complexity (vertical structure) were quantified for each sampling site with the Shannon diversity index (MacArthur and MacArthur, 1961), and their differences were analyzed using a modified t test (Zar, 1999).

## 3. Results

During the dry season 8 sample sites were found with faeces of Chacoan cavies and 10 sample sites in the wet season. For Patagonian maras, faeces where found in 7 and 4 sample sites during the dry and wet season respectively.

### 3.1. Diet

During the dry season, the diet of the Chacoan cavy was richer than the Patagonian mara (41 and 31 species respectively). Most common diet items (over 5% of occurrence in the diet) were similar between both species, but Patagonian mara diet included more grasses species (Table 1). During the wet season, diet richness was also higher for cavies than for maras (52 and 28 species respectively). Three species dominated the diet of Chacoan cavies (over 5% of occurrence in the diet) while 7 species formed the bulk of the diet in Patagonian mara (Table 1). According to diet diversity, cavy's diet was more diverse than mara's in both seasons. Furthermore, diet diversity increased from the dry to the wet season for cavies and decreased for maras (Table 1).

The Patagonian mara consumed more than 80% of monocotyledonous plants in the wet season and 60% in the dry season. On the other hand, Chacoan cavies ate 60% of dicotyledonous in the wet season and 70% in the dry season. In both seasons trees, shrubs, grasses and forbs were consumed in different proportions by both species (Table 2).

Shrubs were the most abundant available resource item during the dry season (57.73%), followed by grasses (20.69%), trees (14.89%), forbs (7.29%), and succulents (2.41%). During the wet season, shrubs were still the most abundant resource (35.07%), but lower than in summer, followed by forbs (27.76%), grasses (20.67%), trees (15.65%) and succulents (0.85%).

We found that diet selection varied with season. During the dry season, maras selected exclusively grasses, whereas cavies selected leaves of trees, grasses, forbs and succulents (Table 3). In the wet season, maras kept the same foraging behaviour, selecting only grasses; whereas cavies changed their foraging behaviour, selecting only grasses as well (Table 3).

### 3.2. Trophic niche

The standardized niche breadth (B$_A$) of cavies was wider than that of maras in both seasons (0.476 and 0.279 respectively for the dry season; 0.305 and 0.246 respectively for the wet season). Both species showed a decrease in niche breadth during the wet season. Niche overlap (PS) was more than 50% in both seasons, and slightly higher during the dry season (0.59 in the dry season and 0.56 in the wet season).

### 3.3. Habitat use

During the dry season both species used habitats with similar variables, but in different proportions, resulting in different habitat structure. The habitat used by maras was dominated by high cover of the lower plant layer (56.91%), followed by litter cover (34.38%), and bare ground (28.74%), whereas cavies' habitat was

**Table 1**
Percentage of occurrence of food items of *Pediolagus salinicola* and *Dolichotis patagonum* during a dry and wet season in Bajondo (Córdoba, Argentina). Values for richness and diversity index (H′) are also shown. *items with percentage of occurrence lower than 1% that where grouped to reduce table.

| Diet Items | Dry season | | Wet season | |
|---|---|---|---|---|
| | *P. salinicola* | *D. patagonum* | *P. salinicola* | *D. patagonum* |
| **Trees** | | | | |
| *Prosopis flexuosa* | 14.75 | 9.54 | 12.12 | 5.73 |
| *Geoffroea decorticans* | 1.15 | 0.06 | 0.93 | 0 |
| *Acacia* sp. | 0.3 | 0.17 | 1.07 | 0.27 |
| *Ziziphus mistol* | 0.5 | 0.74 | 1.24 | 0.27 |
| **Shrubs** | | | | |
| *Mimoziganthus carinatus* | 0.35 | 0 | 2.76 | 0.13 |
| *Lippia turbinata* | 1.25 | 0.46 | 0.36 | 0 |
| *Condalia microphylla* | 3.9 | 0.4 | 1.38 | 0.13 |
| *Senna aphylla* | 13.95 | 12.23 | 6.98 | 5.6 |
| *Suaeda divaricata* | 1.7 | 3.66 | 3.33 | 1.73 |
| *Maytenus vitis-idaea* | 1.45 | 0.06 | 3.02 | 1.6 |
| *Atriplex lampa* | 1.7 | 2.11 | 1.47 | 1.73 |
| *Lycium* sp. | 4.79 | 1.49 | 1.69 | 0 |
| *Schinus fasciculatus* | 0.45 | 0 | 1.38 | 0 |
| Other shrubs* | 3.45 | 0.62 | 5.59 | 0 |
| **Forbs** | | | | |
| *Bidens subalternans* | 0 | 0 | 1.6 | 0.4 |
| *Taraxacum officinale* | 0 | 0 | 2.18 | 0.4 |
| *Dichondra microcalyx* | 3.85 | 0.57 | 3.64 | 0.8 |
| *Alloinia incarnata* | 0 | 0 | 1.16 | 0.13 |
| *Hoffmannseggia glauca* | 0 | 0 | 2.8 | 0.27 |
| Malvaceae NI | 5.12 | 0.34 | 2.22 | 0.67 |
| *Cortesia cuneifolia* | 1.09 | 0.06 | 0.13 | 0 |
| *Pavonia* sp. | 0.5 | 0.06 | 0 | 0 |
| Other forbs* | 0.35 | 0.6 | 4.21 | 0 |
| **Grasses** | | | | |
| *Pappophorum caespitosum* | 5.55 | 14.97 | 1.78 | 8.4 |
| *Cynodon dactylon* | 0.6 | 0.69 | 4.27 | 5.47 |
| *Bouteloua aristidoides* | 0 | 0 | 4.64 | 7.36 |
| *Neobouteloa lephostachya* | 1.5 | 4.74 | 0.65 | 4.11 |
| *Sporobolus indicus* | 1.5 | 1.12 | 14.01 | 28 |
| *Aristida* sp. | 0.5 | 0.51 | 2.98 | 6.8 |
| *Trichloris* sp. | 0.65 | 4.11 | 6.4 | 12.53 |
| *Stipa cordobensis* | 1.9 | 7.89 | 0.27 | 2.67 |
| *Setaria* sp. | 4.75 | 12.8 | 0.4 | 0.13 |
| *Cenchrus myosuroides* | 0.3 | 2.34 | 0 | 0.4 |
| *Cottea pappophoroides* | 0 | 0 | 0.71 | 2.67 |
| *Cyperus* sp. | 0.8 | 0.11 | 0 | 0 |
| Other grasses* | 4.4 | 7.31 | 0.71 | 0.4 |
| **Succulents** | 5.53 | 6.29 | 1.62 | 1.2 |
| **Other Items** | | | | |
| Seeds | 2.25 | 1.3 | 0 | 0 |
| Other dicots NI | 8.15 | 3.13 | 0.3 | 0 |
| Arthropods | 1.2 | 0.06 | 0 | 0 |
| **Diversity Index (H`)** | **1.338** | **1.185** | **1.414** | **1.061** |
| **Richness** | **41** | **31** | **52** | **28** |

characterized by high cover of the lower plant layer (48.52%), litter (41.34%), bare ground (24.4%), and the upper layer (12.52%) (Table 4). In the wet season, maras' habitats were characterized by high cover of the lower layer (58.09%), and two woody layers: trees (27.5%) and shrubs (20%). Cavies' habitats were also dominated by high percent cover of the lower layer (50.79%), followed by shrubs (32.35%), and trees (22.35%) (Table 4). None of these habitat variables were statistically different ($p > 0.05$) between species in either season. Habitat heterogeneity was similar between species and between seasons. Nevertheless, habitats used by cavies were significantly more complex than those used by maras in the wet season (Table 5).

## 4. Discussion

During sampling, signs of presence of both species were not abundant, reflecting low population densities in the region. This may be due to the fact that the Dry Chaco region constitutes the southern and northern geographic ranges of *P. salinicola* and *D. patagonum* respectively (Fig. 1). Consequently, under the abundant-centre hypothesis (Brown, 1984) the availability of optimal habitats are less frequent in their limits of distribution and species occupying marginal habitats are less abundant than in the centre of their geographic range. Under this situation, the accelerated degradation of the region due to grazing pressure, logging and fire may decrease the availability of "suitable" habitats for both species, having a negative influence on their abundances.

In this marginal region of their distributional area, our results support the niche partition hypothesis, where morphologically, ecologically and closely related sympatric species segregate in at least one of the niche dimensions to allow coexistence. Diet and habitat analyses indicate that *P. salinicola* and *D. patagonum* segregate in the use of the trophic niche dimension during both seasons, whereas habitat was only slightly segregated during the wet season. These coexistence mechanisms were also verified in a diversity of mammal taxa, with segregation in one or more of the three main niche dimensions (diet, habitat and time) (Meserve, 1981; Wei et al., 2000; Bryce et al., 2002; Almeida Jácomo et al., 2004; Garcia and Arroyo, 2005; Davies et al., 2007; DiBitetti et al., 2009), with the diet dimension being the most commonly segregated niche axis among herbivores (Luo and Fox, 1996; Cortés et al., 2002; Stewart et al., 2002; Prins et al., 2006).

As Hutchinson predicts (1957), species broaden their trophic niches when resources are less abundant (dry season). Our study supports this for both species. On the other hand, we expected niche overlaps between mara and cavy to be higher in the dry season. However, niche overlap was the same in the dry and wet season. This is possible only if one or both species change their foraging behaviour (Pianka, 1981). In our study, the Chacoan cavy changed its foraging strategy between seasons, selecting leaves of trees, forbs, grasses and succulents during the dry season and selecting only grasses during the wet season when this item is more available. Patagonian mara, on the other hand, selected only grasses

**Table 2**
Mann−Whitney non parametric test for plant life forms between diets of *Pediolagus salinicola* and *Dolichotis patagonum* during a dry and wet season in Bajondo (Córdoba, Argentina). Mean and standard error are shown as X (SE). *Significant differences ($p < 0.05$).

| Variable | Dry season | | | Wet season | | |
|---|---|---|---|---|---|---|
| | *P. salinicola* | *D. patagonum* | *p* | *P. salinicola* | *D. patagonum* | *p* |
| Trees | 16.7 (6.39) | 10.51 (4.17) | 0.015* | 15.41 (5.07) | 6.27 (2.51) | 0.0091* |
| Shrubs | 32.39 (3.24) | 20.52 (2.86) | 0.002* | 27.91 (1.76) | 10.93 (1.37) | 0.0182* |
| Grasses | 22.45 (1.89) | 56.59 (4.97) | 0.0003* | 36.81 (3.86) | 78.93 (7.48) | 0.0091* |
| Forbs | 10.91 (1.36) | 1.09 (0.14) | 0.0003* | 18.21 (1.09) | 2.67 (0.24) | 0.0091* |
| Succulents | 5.35 (1.09) | 6.29 (4.45) | 0.887 | 1.62 (0.97) | 1.2 | 0.923 |

**Table 3**

Maximum and minimum values of Confidence intervals for life forms in *Pediolagus salinicola* and *Dolichotis patagonum* diets during a dry and wet season in Bajondo (Córdoba, Argentina). †: selected items; ‡: not selected items; §: items consumed according to availability.

| Variables | Dry Season | | Wet Season | |
|---|---|---|---|---|
| | P. salinicola | D. patagonum | P. salinicola | D. patagonum |
| Trees | 1.15–1.09† | 0.74–0.66‡ | 1.04–0.97§ | 0.48–0.32‡ |
| Shrubs | 0.61–0.59‡ | 0.4–0.36‡ | 0.80–0.78‡ | 0.34–0.29‡ |
| Grasses | 1.1–1.06† | 2.74–2.72† | 1.81–1.78† | 3.82–3.80† |
| Forbs | 1.66–1.55† | 0.51–(−0.21) ‡ | 0.64–0.61‡ | 0.21–(−0.02) ‡ |
| Succulents | 2.52–1.92† | 1.24–(−0.48) § | 4.52–(−0.67) § | 5.08–(−2.27) § |

all year round. These foraging patterns reflect generalist behaviour for cavies during the season of reduced food availability, but specialist behaviour on grasses for maras.

When alone, Chacoan cavy acts as a generalist herbivore with a diet strongly influenced by the availability of resources. They preferred dicots, with leaves of forbs and shrubs being the most consumed items across their distributional range (Rosati and Bucher, 1995). The Patagonian mara, nevertheless, changed its diet along its geographical range, eating leaves of shrubs and forbs in the southern part (Bonino et al., 1997), and leaves of grasses in the central-northern part (Kufner and Pelliza de Sbriller, 1987; Campos et al., 2001b; Sombra and Mangione, 2005; Rodríguez and Dacar, 2008). These differences where more pronounced due to the sympatric relationship with the cavy, where niche differentiation is associated to the type of items consumed. In our study site, maras always ate more monocots than cavies, which allow us to characterize the mara as a grazer, with a homogeneous behaviour throughout the year. The cavy has a more flexible diet throughout the year, and can be considered to be an opportunistic browser. These foraging strategies allow both species to coexist in an area where presence of cattle and intense dry periods diminish plant availability.

In this sympatric region, habitat resource was not markedly segregated. Both species used habitats with the same structural characteristics. Nevertheless, when comparing habitat structure as a measure of complexity, during the wet season Chacoan cavies

**Table 4**

Percentage of cover of 16 habitat variables measured in areas used by *Pediolagus salinicola* and *Dolichotis patagonum* during a dry and wet season in Bajondo (Córdoba, Argentina).

| Variable | Dry Season | | Wet Season | |
|---|---|---|---|---|
| | D. patagonum (%) | P. salinicola (%) | D. patagonum (%) | P. salinicola (%) |
| Bared soil | 28.74 | 24.40 | 15.51 | 7.88 |
| Litter | 34.38 | 41.37 | 19.45 | 20.86 |
| Trees | 18.11 | 12.55 | 27.50 | 22.35 |
| Shrubs | 13.12 | 17.67 | 20.00 | 32.95 |
| Grasses | 2.93 | 2.81 | 11.96 | 7.84 |
| Forbs | 1.84 | 1.00 | 5.54 | 8.23 |
| Succulents | 0.87 | 0.20 | 0.00 | 0.00 |
| 0–25 cm (first layer) | 56.91 | 48.52 | 58.09 | 50.79 |
| 25–50 cm | 5.00 | 3.25 | 11.07 | 7.11 |
| 50–75 cm | 4.55 | 3.79 | 8.03 | 5.64 |
| 75–100 cm | 4.19 | 5.18 | 6.95 | 5.31 |
| 100–125 cm | 6.24 | 7.04 | 4.34 | 6.14 |
| 125–150 cm | 5.08 | 6.68 | 3.47 | 5.67 |
| 150–175 cm | 4.55 | 6.08 | 2.93 | 5.31 |
| 175–200 cm | 5.35 | 6.92 | 2.71 | 4.49 |
| >200 cm (upper layer) | 8.12 | 12.52 | 2.39 | 9.55 |

**Table 5**

Complexity and Heterogeneity indices for habitats used by *Pediolagus salinicola* and *Dolichotis patagonum* during a dry and wet season in Bajondo (Córdoba, Argentina). *Significant differences in t test between species in each season ($p < 0.05$).

| | | D. patagonum | P. salinicola | t |
|---|---|---|---|---|
| Dry Season | Complexity | 0.691 | 0.748 | 1.214 |
| | Heterogeneity | 0.625 | 0.618 | 0.201 |
| Wet Season | Complexity | 0.647 | 0.739 | 2.138* |
| | Heterogeneity | 0.737 | 0.71 | 1.546 |

used more vertically complex habitats than the Patagonian mara. This difference in habitat use is also evident when these species occur alone. The Patagonian mara uses open habitats with sparse vegetation (Kufner and Chambouleyron, 1991; Gonnet, 1998; Baldi, 2007; Tabeni, 2006; Rodriguez, 2009), keeping this preference stable along their geographic range. Chacoan cavies also use open habitats but they are more flexible in their strategy, occupying habitats with higher plant cover when open ones are not available (Rosati and Bucher, 1995). The Chaco region (where Chacoan cavies occur exclusively) is more complex than the Monte (where maras occur exclusively), thus segregation of Chacoan cavies to a more complex habitat during the wet season is consistent with their optimal environment.

To summarize, during the dry season in the Dry Chaco both species segregated diet but not habitat niche; and during the wet season these species segregated their habitat and diet niche segregation was more diffused. This complementarity in the segregation of niche dimensions is predicted by the niche partition hypothesis (Schoener, 1974) and it occurs also in other herbivores living in sympatry (Luo and Fox, 1996; Stewart et al., 2002; Cortés et al., 2002; Prins et al., 2006). Because of continuing anthropogenic disturbance in the Dry Chaco (deforestation, fire and cattle), complexity of this system has diminished, with woodlands having been transformed into open shrublands (Karlin et al., 1994). For this reason, the region presents habitat characteristics intermediate between Chaco and Monte. These intermediate habitat characteristics may be an excellent scenario for both species to be sympatric in the marginal regions of their distribution. Under this scenario, niche segregation plays an important role in facilitating the coexistence of these phylogenetically and ecologically related species.

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