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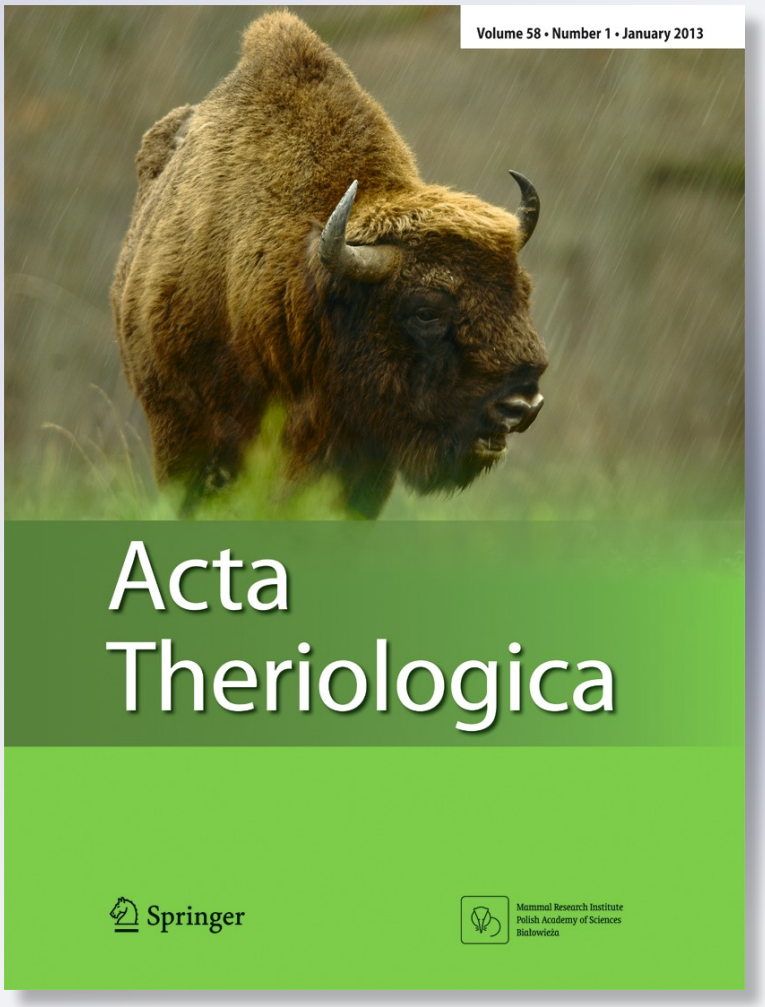

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ORIGINAL PAPER

Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina

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Abstract The wild boar, *Sus scrofa*, was first introduced for hunting purposes in Argentina in 1906 and presently occupies a wide range of habitats. Understanding the food habits of invasive species is important for predicting the effects of animal food consumption on the environment and on human activities, such as farming. The wild boar is an omnivorous, opportunistic species whose diet is determined by the relative abundance of different types of foods. In general, the wild boar's diet has been widely studied in the world, both as a native and invasive species, but little is known regarding food resource selection in the Monte Desert biome. Our study assessed the seasonal variation in the diet of wild boars, as well as the nutritional quality of consumed items. Further, we determined the diet selection of this species. Diet analyses were based on faecal samples collected over two seasons (wet and dry) in 1 year. Herbs were the most frequently consumed food item, with wild boars showing a selection for them in both seasons. The wild boar uses food resources according to seasonal availability (larger trophic niche breadth under higher plant diversity, as in the wet season). In turn, within each season, it selects items of high forage quality and high carbohydrate contents. In conclusion, this foraging strategy enables wild boar to maximize energy budget through food selection in order to survive in a semi-arid environment such as the Monte Desert.

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Keywords Diet selection · *Sus scrofa* · Seasonal variation · Invasive species · Arid lands

Introduction

The feeding habit of an animal species is a fundamental trait of its ecological niche and is a basic aspect in the study of the species' ecology (Johnson 1980). Knowledge of diet not only contributes to information related to the energy that individuals need to survive and breed, but also leads to insights about the interactions between the consumer species and its environment, as well as interspecific interactions within the community (predation, competition, etc.; Sih and Christensen 2001). The study of diet composition of a given species is important to determine food categories, item selection, seasonal variation, as well as to predict when and how some plant communities may be damaged (Wood and Roark 1980). In addition, it is important both for conservation of a particular species by determining its specific requirements and for management of invasive species by predicting the effects of food consumption on the environment and on human concerns such as crop yields (Baubet et al. 2004). Diet composition can help understand how animals use different habitats, to determine the ecological role of species, and their place within food webs (Baubet et al. 2004).

According to the optimal diet theory, individuals select their food in order to maximize their net rate of energy intake while foraging (Sih and Christensen 2001). Ultimately, this is going to depend on the abundance, energy contents and handling time of food (Pulliam 1980). Foraging behaviour could have a significant effect on the regeneration of vegetation. For example, most Suidae (pigs) influence plant regeneration through seed consumption and digging, as they can bury

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seeds as well as uproot seedlings and other plants (Danell et al. 2006).

Food resource constraints occur mainly during the dry season, when low plant abundance and quality generate weight loss in animals, with survival depending on the body fat reserves gathered during the last favourable period (Danell et al. 2006). This is more accentuated in arid environments, where most of the plants have low nutritional value (Noy-Meir 1973). Also, environmental conditions in arid and semi-arid lands are extreme, and species are generally subjected to seasonal and spatial variation of several resources (van Horne et al. 1998). This heterogeneity, added to the manner in which animals select their food, especially in periods of scarcity, can have important consequences for the species' population dynamics (Ostfeld and Keesing 2000).

Biological invasions are considered one of the main threats to natural ecosystems (Vitousek et al. 1997). A primary focus of invasion biology is to assess the impact of exotics on native species, communities and ecosystems (Williamson 1996). The wild boar, *Sus scrofa*, was first introduced in Argentina in 1906 for hunting purposes (Daciuk 1978). Presently, the wild boar occupies a wide range of habitats, from the Patagonian forests and humid pampas to arid and semi-arid regions of the country. The negative effects of the wild boar as both an invasive species and an ecosystem engineer are well-known around the world, not only for the damage inflicted to agricultural crops (Seward et al. 2004; Wilson 2004), but also on the native biota (Arrington et al. 1999; Bratton 1975; Singer et al. 1984; Tierney and Cushman 2006). In the northern Patagonia region of Argentina, previous studies show that the wild boar causes a reduction in seed survival and seedling regeneration of the native conifer *Araucaria araucana* (Sanguinetti and Kitzberger 2010). In addition, in the Monte Desert biome, wild boar rooting significantly reduces plant cover of herbs, perennial grasses and shrubs and decreases plant richness and diversity (Cuevas et al. 2012). Further, disturbed soils in the same study site showed less compaction, more moisture, a lower *C*/*N* ratio and higher content of mineral nitrogen, thus generating an increase in soil degradation by wind erosion.

The wild boar is an omnivorous, opportunistic species whose diet is determined by the relative abundance of different types of foods (Schley and Roper 2003). It prefers plant material rich in energy, namely with high content of carbohydrates and fats (Massey et al. 1996). Although its diet includes a wide variety of roots, bulbs, herbs, small vertebrates and invertebrates, it is mainly based on plant matter (between 87 and 99 %). As for the latter, the consumed parts of plants are known to vary seasonally. In general, in humid environments such as forests in Europe, USA and New Zealand, during winter and autumn, wild boars feed mainly on mast such as acorns, chestnuts and beechnuts and belowground parts such as roots and bulbs. Alternatively, in summer and spring, they select aerial parts of herbs and grasses and in minor proportion belowground parts (Baubet et al. 2004; Durio et al. 1995; Eriksson and Petrov 1995; Fournier-Chambrillon et al. 1995; Giménez-Anaya et al. 2008; Howe et al. 1981; Taylor 1999; Thompson and Challies 1988; Wood and Roark 1980). On the other hand, there are several wild boar populations that prefer feeding almost exclusively on crops (Giménez-Anaya et al. 2008; Herrero et al. 2006). This implies that when crops are available (including corn, wheat and sunflower), wild boars use those resources in large quantities.

Studies on wild boar's diet in arid lands are scarce, but the tendency seems to be similar to the above. For these places, the seasonal variation of diet depends on rainfall. During the wet season, wild boars feed mainly on aerial parts of herbs and grasses, while in the dry season, fruits and belowground parts are the most important food items (Adkins and Harveson 2006; Baber and Coblentz 1987; Barrett 1978; Taylor and Hellgren 1997). In these cases, animal matter content is low but always present, and its proportion in the diet varies between 1.3 and 8.9 %.

Wild boars make seasonal movements according to their specific requirements, showing a larger home range during low-resource seasons than in seasons with high-resource availability (Bertolotto 2010; Hayes et al. 2009; Singer et al. 1981). These changes in home range generate a seasonal variation in diet, with a more diverse diet (broader trophic niche) during the low-resource season (Massey et al. 1996). Although this species has opportunistic and generalist habits, it has a tendency to select a few abundant, digestible and nutritious elements. This, coupled with its high ecological plasticity, allows it to consume a variety of food sources based on their availability (Rosell et al. 2001).

In Argentina, there is only one study of wild boar's diet which showed that the dry season diet is composed of 95 % of plant matter, out of which, 75 % are herbs (Cuevas et al. 2010). However, that study did not include seasonal variation in food resources or diet selection. Since the wild boar lacks sweat glands, its water requirements are compensated with water from metabolic pathways, preformed water in food and free available water in the environment (Rosell et al. 2001). This fact, coupled with the absence of crops in the study area, highlights the importance of determining the diet of wild boar in the Monte Desert, especially in order to understand how this species compensates for part of its water requirements in arid environments. Therefore, the objectives of this study were to: (1) determine the composition of wild boar's diet and analyse whether there is seasonal variation in food consumption, (2) determine whether there is food selection by wild boar and (3) assess the nutritional quality of consumed items.

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Methods

Our study was conducted in the central region of the Monte Desert, at the Man and Biosphere Reserve of Ñacuñán (34° 02′ S, 67°58′ W; Fig. 1) in Mendoza Province, Argentina. The landscape is characterized by a heterogeneous mosaic of vegetation patches and covers 12,300 ha. Dominant habitats are known as "algarrobal" or *Prosopis* woodland, "jarillal" or *Larrea* shrubland and "medanal" or sand dunes (Roig and Rossi 2001; Rossi 2004). *Prosopis* woodlands are formed by three-layer patches with *Prosopis flexuosa* as a main component of the tree layer, accompanied by a shrub layer of *Larrea divaricata*, *Condalia microphylla*, *Lycium tenuispinosum*, *Junellia aspera* and *Capparis atamisquea* and a lower layer dominated by grasses like *Pappophorum caespitosum*, *Digitaria californica*, *Sporobolus cryptandrus* and forbs such as *Sphaeralcea miniata* and *Verbesina encelioides*. This habitat represents 69 % of the reserve. *Larrea* shrublands are characterized by the presence of few or no trees and high canopy cover of shrubs, mostly *Larrea cuneifolia*, and grasses such as *Trichloris crinita* and herbs that form colonies like *Pitraea cuneato-ovata*, *Kallstroemia tucumanensis* and *Glandularia mendocina*. This habitat represents 24 % of the reserve. Sand dunes are characterized by low cover of shrubs (*Ximenia americana* and *L. divaricata*) and grasses (*Aristida mendocina*, *Panicum urvilleanum* and *Portulaca grandiflora*, among others) and represent the remaining 7 % of the reserve.

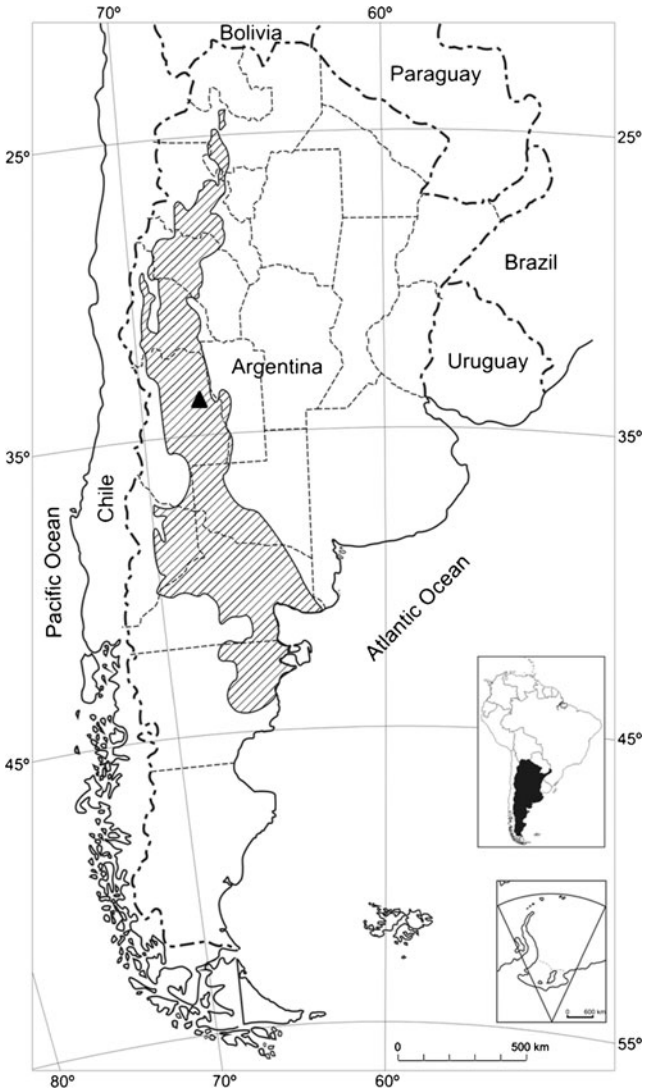

Fig. 1 Monte Desert biome and geographic location of the Man and Biosphere Reserve of Ñacuñán

The landforms consist of an undulating to depressed loess-like sandy plain of quaternary fluvial, lacustrine and aeolian origin (Abraham et al. 2009). The climate is semi-arid and strongly seasonal, with hot humid summers and cold dry winters. Mean annual precipitation is 326 mm. Mean annual temperature is 15.6 °C, with a maximum annual mean of 23.8 °C and a minimum annual mean of 7.6 °C. The wet season is from November to April and the dry season spans from May to October (Claver and Roig-Juñent 2001; Labraga and Villalba 2009).

Sampling design

To determine the composition of wild boar's diet, we collected fresh faeces along 80 transects of 1 km length and in inner and perimeter trails of the reserve. Along each transect, we randomly set up 50 m^2 (10×5 m) plots where plant species composition and plant cover were recorded using modified point-quadrat method across two transects of 10 m length (Passera et al. 1983).

Diet analysis

We used faeces for diet analysis instead of stomach contents because animal trapping and killing are not allowed in the protected area. Ten grams from each faecal sample was analysed using a modified microhistological technique (Dacar and Giannoni 2001) that allows identification of leaf epidermis, stems, seed teguments, fruits, arthropod body parts, rhizome tissues and mammal hairs. For each sample, we prepared one microscope slide and systematically examined 50 fields under microscope at ×40. In a previous analysis, the number of fields to observe proved to be adequate and representative for this purpose (Dacar, personal communication). Food items in the faecal samples were identified by comparison with reference material. Only plant items were identified to species level when possible. Presence of a food item was recorded, and its relative frequency of occurrence per slide was determined by dividing the number of microscope fields in which that item occurred by the total number of microscope fields observed ×100 (Holechek and Gross 1982). Although faeces are

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subjected to a higher digestive activity than stomach contents, they still contribute pertinent qualitative information on diet (Barreto et al. 1997; Rudge 1976).

We assessed the adequacy of sample size by the method proposed by Milanesi et al. (2012). We calculated the Brillouin index according to the equation:

$$H_b = \frac{\ln N! - \sum \ln n_i!}{N}$$

where N is the total number of food items registered in all samples and n_i is the number of individual food item in the ith category (Magurran 1988). The index ranges from 0 to 4.5. A diversity curve was then calculated by increments of two samples randomly taken. For each sample, a value for H_b was calculated and then resampled 1,000 times to obtain a mean and 95 % confidence interval. Adequacy of sampling size was determined by whether an asymptote was reached in the diversity curve and another curve calculated from the incremental change in each H_b with the addition of two more samples. Both curves were plotted against the number of analysed scats.

Seasonal variation and diet selection

To determine whether there was seasonal variation in the consumption of different plant parts, we clustered the consumed items into four categories: aerial parts (leaves and stems), belowground parts (bulbs and roots), fruits (seeds and fruits) and animal matter and then applied the Kolmogorov–Smirnov test to detect significant differences between seasons (Zar 1999). We used Levins' B index, standardised by Hurlbert (1978), to determine trophic niche breadth for each season:

$$B_s = \left(\frac{1}{\sum p_i^2}\right) - 1/(n-1)$$

where p_i is the relative proportion of item i in the diet of wild boar, and n is the number of item taxa. This index ranges from zero to one.

We only used plant matter to assess diet selection. Plant species were clustered into five categories according to life form: herbs, grasses, sub-shrubs (shrubs less than 1 m tall), shrubs and trees. Food availability was calculated by estimating the proportion of each food category (herbs, grasses, sub-shrubs, shrubs and trees) from the plots randomly set up along the transects. Wild boar selection was estimated by applying the Manly's index of selectivity (Manly et al. 2002):

$$\alpha_i = \frac{Pu_i}{Pa_i} x \frac{1}{\sum \frac{Pu_i}{Pa_i}}$$

where Pu_i is the observed proportion of item i in the wild boar's diet and Pa_i is the available proportion of item i in the environment. If α_i is greater than $1/k$, being k the number of food items, then item i is selected. If α_i is less than $1/k$, then the item i is avoided. To test the reliability of the Manly's index, we resampled boar faeces 1,000 times by bootstrapping. We then calculated the average values and the 95 % confidence intervals of the Manly's index. The 95 % confidence intervals that include the value $1/k$ indicate a use that is proportional to the availability.

Nutritional value of food items in wild boar's diet

Finally, to evaluate if consumed food items have a high nutritional content, a bibliographic search was conducted. The data collected was summarized in a table that included the nutritional values of those species found in wild boar's diet. For each food item, we recorded its nutritional relationship, forage value, percentage of proteins, fats, fibres and non-nitrogen compounds. The nutritional relationship is the ratio between protein and fat, fibre and non-nitrogen compounds. This ratio determines how good a plant is as livestock forage (Candia 1980). A close nutritional relationship (low values) implies a higher protein content, which means a better quality of forage. The opposite occurs with fibre, which is inversely related to digestibility (Noblet and Pérez 1993), so that when the percentages of fibre, fat or non-nitrogen compounds are high, the nutritional relationship has high values and this entails lower forage quality.

Results

Diet description

We collected a total of 26 faeces of wild boar during the wet season and 25 faeces during the dry season. In both seasons, the diversity curves reached an asymptote and the incremental change declined to <1 % at ≥15 samples (Fig. 2), indicating that the sampling effort was adequate.

During the wet season, microhistological analyses showed that 94.3 % of the diet was composed of plant matter (29 plant species) and the remaining 5.7 % corresponded to animal matter (arthropods and mammals). Forty-five percent of the plant matter was composed of herb species, followed by 33.6 % of woody species (shrubs and trees), grasses (12.1 %) and cacti (3.6 %) (Fig. 3). Within the herbs category, seeds of *S. miniata* and bulbs of *P. cuneato-ovata* were the most frequent items (28.2 and 4.8 %, respectively). Of the consumed woody species, 13.2 % corresponded to fruits of *P. flexuosa* and 8.8 and 6.6 % were leaves of *Junellia seriphioides* and *Lycium* sp., respectively. Within the grass category, none of the species exceeded 3 %. Regarding the composition of the diet in terms of plant parts, we found that fruits were the most frequent item with

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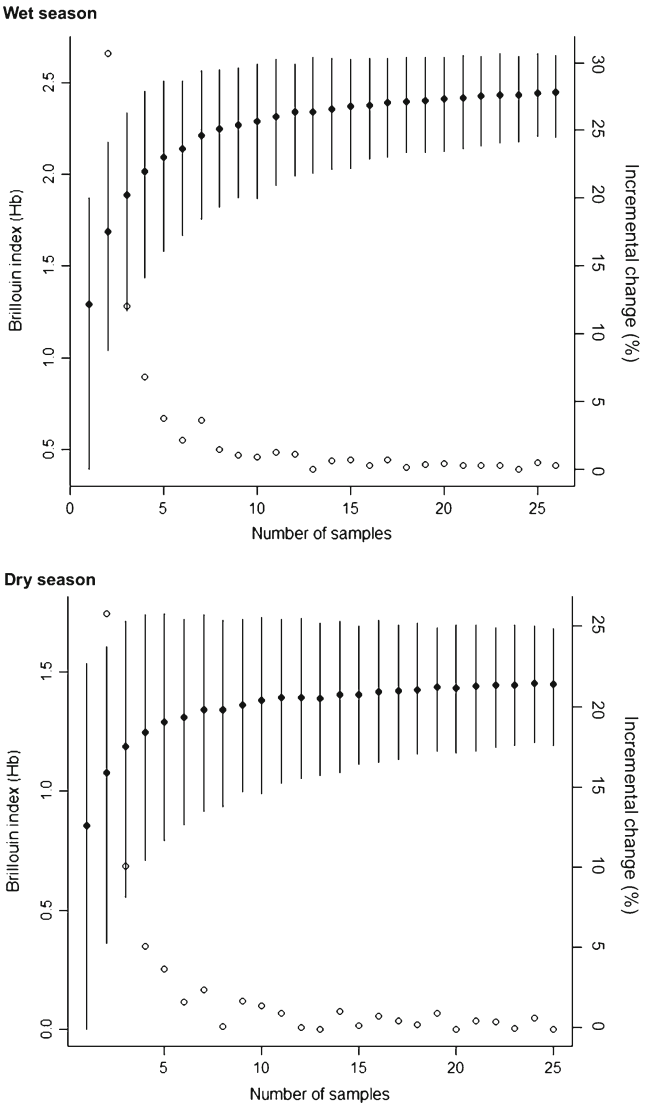

Fig. 2 Diversity curves and incremental change curves for wild boars faeces during wet and dry seasons. Mean and 95 % confidence intervals obtained by resampling with replacement 1,000 times

47.9 %, followed by aerial parts (38.5 %) and belowground parts (7.9 %) (Fig. 4).

During the dry season, we identified 21 plant species which represented 98.5 % of the diet and only 1.5 % was animal matter. The bulk of the diet consisted of herb species (65.6 %), followed by woody species (23.1 %), cacti (5.2 %) and grasses (4.6 %) (Fig. 3). Within the herb category, 57.9 % were leaves and seeds of *S. miniata*, and 4.9 % corresponded to bulbs of *P. cuneato-ovata*. Among the woody species, *P. flexuosa* (mainly leaves and seeds) was the most frequent food item (17.8 %). Within the grass category, none of the species exceeded 2.7 %. Regarding the different parts of plants, we found that 68.7 % were aerial parts, while the remaining 19.8 and 10.1 % corresponded to fruits and belowground parts, respectively (Fig. 4).

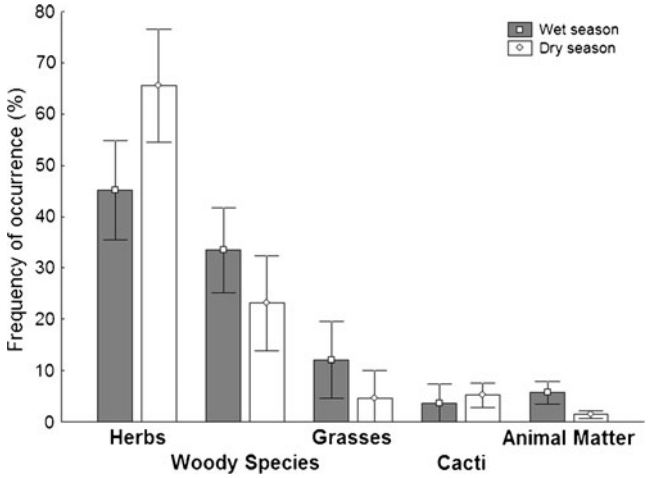

Fig. 3 Frequency of occurrence (mean±2SE) of each food items in wild boar diet during wet and dry seasons in central Monte Desert, Argentina

Seasonal variation and diet selection

We found significant differences between seasons in wild boar's diet for the categories aerial parts, fruits and animal matter (Fig. 4). Aerial parts were consumed more frequently during the dry season, whereas during the wet season, fruits and animal tissue were more frequent. The standardised niche breadth of wild boars was wider during the wet season (H_b=0.176) than in the dry season (H_b=0.075).

The result of the trophic selection analysis via the Manly's index showed that herbs were selected in both seasons while grasses, sub-shrubs and shrubs were avoided. The trees were used as available during the wet season, but were avoided in dry season (Fig. 5).

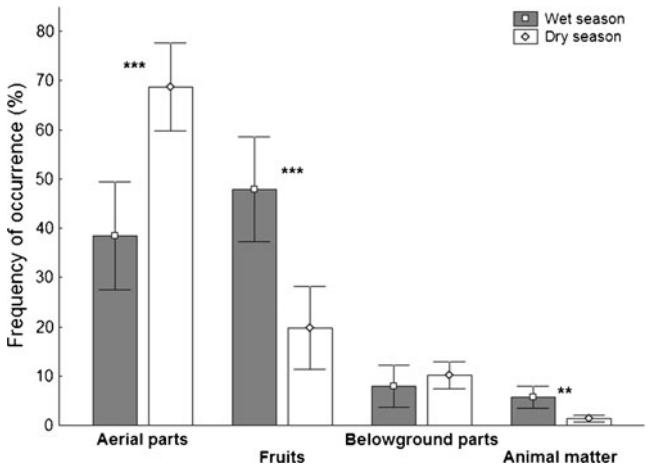

Fig. 4 Seasonal variation (mean±2SE) in the consumption of the different parts of plants found in wild boar diet in central Monte Desert, Argentina (**p<0.01, ***p<0.001)

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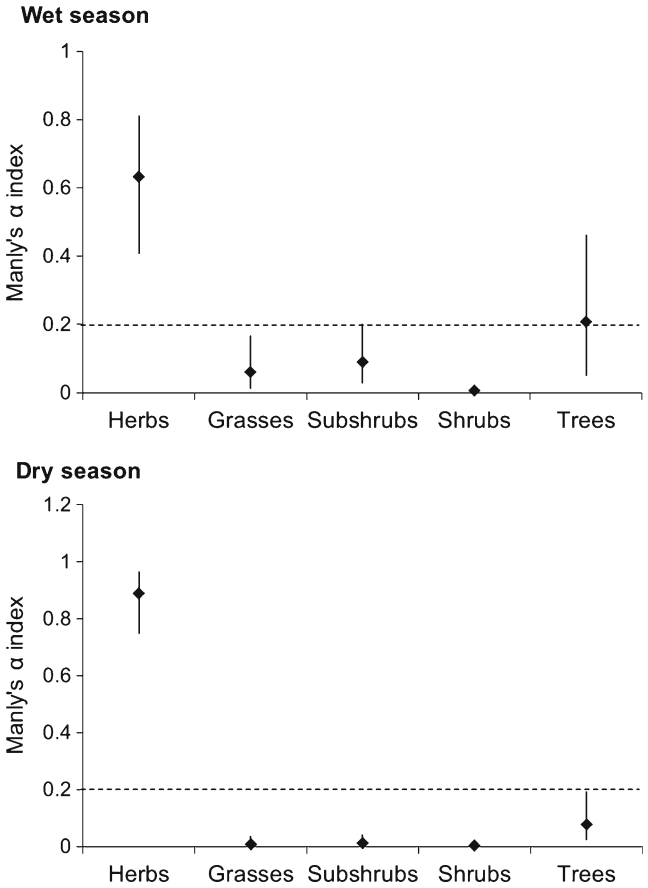

Fig. 5 Manly's selectivity index (±95 % CI) for food categories during wet and dry seasons. *Dotted line* indicates $1/k=0.2$ for a use proportional to the availability

Nutritional value of food items in wild boar's diet

We found complete nutritional values (percentage of protein, fat, fibre and non-nitrogen compounds, nutritional relationship and forage value) for 22 species of the 35 species considered. We did not find complete information for 11 species and did not find any data regarding the roots of *Cereus aethiops*, *Doniophyton patagonicum* and *Opuntia sulphurea* (Table 1).

We included the nutritional values of alfalfa (*Medicago sativa*), a forage of excellent quality, for comparison. For those species that we obtained complete information, we found that three species have "exceptional" forage value, five species have "outstanding", five have "very good", three have "good", four have "medium" and two have "low" forage value (Braun and Candia 1980; Candia 1980; Guevara et al. 1991; Rossi et al. 2008; Silva Colomer et al. 1991; Stasi and Medero 1983; Van den Bosch et al. 1997; Wainstein et al. 1979; Wainstein and González 1963; Wainstein and González 1971a; b). Considering only the percentage of proteins and fibres, we found that most of the food items have good nutritional quality (Noblet and Pérez 1993).

Given that that the most frequent food items in wild boar's diet were *S. miniata*, *C. atamisquea*, *Chloris castilloniana*, *Descurainia* sp., *Setaria* sp., *Lycium* sp., fruits of *P. flexuosa* and bulbs of *P. cuneato-ovata*, we observe that, except for the two last, these species have a very good forage value. Indeed, the most frequently consumed plant during both seasons, *S. miniata*, has the highest forage value (exceptional). Bulbs of *P. cuneato-ovata* have a very low forage value (low), which is due to their high content of carbohydrates (Stasi and Medero 1983).

Discussion

The wild boar's diet in the Monte Desert was composed mainly of plant matter; this being 94.3 % of the total diet during the wet season and 98.6 % in the dry season. The high content of plant material and the low percentage of animal matter in wild boar's diet have been previously reported by other authors for different habitat types in different parts of the world, including places where this species is native and where it is exotic (Adkins and Harveson 2006; Baber and Coblentz 1987; Baubet et al. 2004; Cuevas et al. 2010; Durio et al. 1995; Eriksson and Petrov 1995; Fournier-Chambrillon et al. 1995; Giménez-Anaya et al. 2008; Herrero et al. 2006; Howe et al. 1981; Massey et al. 1996; Schley and Roper 2003; Skewes et al. 2007; Taylor 1999; Taylor and Hellgren 1997; Thompson and Challies 1988; Wood and Roark 1980).

In this study, the most frequent food items in the wild boar's diet during both seasons were herbs (45.2 % in wet season and 65.6 % in dry season), followed by woody species (33.5 and 23.1 %, wet and dry season, respectively). Cuevas et al. (2010) reported similar results for the dry season in the Monte Desert biome: 95 % of the diet being plant material and the remaining 5 % corresponding to animal matter. In addition, herb species constituted the bulk of the diet (64.2 %), followed by woody species (21.6 %), fruits (14.2 %) and grasses (9.1 %). In relation to other arid zones invaded by wild boars, such as southeast Texas (USA), Adkins and Harveson (2006) found that herbs were the most consumed food item during the wet season (38.6 %), followed by bulbs and roots (34.3 %). Taylor and Hellgren (1997) indicated that in northeast Texas, wild boars feed mainly on grasses (66 %) during the wet season and on bulbs and roots (61 %) in the dry season. While in California (USA), they consume mainly fruits (45 %) in both seasons (Barrett 1978; Baber and Coblentz 1987), our results showed that grasses represented low percentages in both seasons, whereas fruits were found with high frequency in wet season, and belowground parts of plants did not exceed 10 % in either season.

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Table 1 Nutritional values of food items present in wild boar's diet in central Monte Desert, Argentina

Species	Total proteins (%)	Fats (%)	Fibre (%)	Non-nitrogen compounds (%)	Nutritive relation 1	Forage value
Alfalfa (*Medicago sativa*)	26.74	2.19	39.65	35.69	2.01	Exceptional
Adesmia filipes	12.10	1.62	29.31	30.32	5.20	Outstanding
Bouteloua aristidoides	7.65	1.63	32.77	40.87	10.10	Medium
Bromus brevis	11.00	1.82	32.10	36.63	6.60	Very good
Capparis atamisquea	20.12	2.00	32.09			
Condalia microphylla	13.25					
Cottea pappophoroides	9.32	1.60	30.20	40.61	8.00	Medium
Chenopodium papulosum	13.30	1.96	23.94	33.54	4.60	Outstanding
Chloris castilloniana	11.08	2.04	28.40	40.00	6.50	Very good
Descurrainia sp.	22.40		23.8			
Digitaria californica	7.91	1.89	35.00	39.84	9.90	Medium
Fabiana peckii	5.60		39.00			
Geoffroea decorticans	21.26		28.66			
Gomphrena martiana	13.20	3.79	24.89	31.76	4.90	Outstanding
Gomphrena tomentosa	10.08	1.13	25.28	31.64	5.90	Very good
Junellia aspera	4.38					
Junellia seriphioides	4.30		47.10			
Larrea divaricata	15.63		21.16			
Larrea cuneifolia	17.10		22.63			
Lecanophora ecristata	11.73	1.96	31.09	35.41	6.00	Very good
Lycium chilense	12.97	3.88	25.33	34.73	5.30	Outstanding
Panicum urvilleanum	9.50	1.58	32.79	37.70	7.80	Good
Pappophorum philippianum	8.57	1.19	29.50	42.50	8.70	Medium
Pitraea cuneato-ovata (leaves)	15.31	6.97	11.24	36.98	4.60	Outstanding
Pitraea cuneato-ovata (bulbs)	7.80	1.35	31.50	39.03	14.06	Low
Poa lanuginosa	20.90					
Prosopis flexuosa (leaves)	17.98		44.32			
Prosopis flexuosa (fruits)	11.36	3.95	18.65	56.01	7.20	Good
Setaria leucopila	12.03	2.02	28.40	39.51	6.00	Very good
Sphaeralcea miniata	16.93	2.13	23.39	35.60	3.80	Exceptional
Stipa tenuis	7.30	1.96	1.96	38.57	11.10	Low
Trichloris crinita	9.60	1.65	31.40	39.01	7.60	Good
Verbesina encelioides	19.5	4.26	19.07	27.76	2.90	Exceptional

Alfalfa values are for comparison

The seasonal variation of wild boar's diet in arid lands, where they are also an invasive species, showed a higher consumption of aerial parts during the wet season (or spring–summer season), while fruits and belowground parts were higher in the dry season (or autumn–winter season) (Adkins and Harveson 2006; Baber and Coblentz 1987; Barrett 1978). This also occurs in those places where the wild boar is native (Baubet et al. 2004; Durio et al. 1995; Eriksson and Petrov 1995; Fournier-Chambrillon et al. 1995; Giménez-Anaya et al. 2008; Howe et al. 1981; Taylor 1999; Taylor and Hellgren 1997; Thompson and Challies 1988; Wood and Roark 1980). However, in our study and in contrast with other studies, wild boars consumed more aerial parts during the dry season and more fruits and animal matter during the wet season.

On the other hand, there are several works that show a frugivorous trend in wild boars as both a native (Durio et al. 1995; Eriksson and Petrov 1995; Fournier-Chambrillon et al. 1995; Irizar et al. 2004) and exotic species (Thompson and Challies 1988; Wood and Roark 1980). In our study, fruits were present in both seasons but were more frequent during the wet season. The differences in fruit consumption may be because fruiting of plant species in the Monte Desert occurs during the wet season, so fruit availability is higher (Rundel et al. 2007). Regarding animal content in wild boar's diet, in California (Baber and Coblentz 1987) and in Texas (Taylor and Hellgren 1997), an increased consumption of animal matter was also registered during the wet season (9 versus 0 % during the dry season for the

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California study and 12 versus 6.5 % in the dry season for the study of Texas). Although animal matter is low, it is always present in the diet of wild boar (Schley and Roper 2003) and our results showed the same pattern. This could be because although wild boar eats mostly plant material, the content of dietary protein obtained from animal matter is important for its growth and survival (Schley and Roper 2003), especially in arid and semi-arid ecosystems where the majority of plants have low nutritional value due to their high fibre content (Noy-Meir 1973).

In a Mediterranean forest and scrubland environment of central Italy, where the wild boar is native, Massey et al. (1996) reported that this species expands its dietary range during the season of low-resource availability. Our results showed a higher trophic niche breadth during the wet season (i.e. high available of food resources), which could indicate that the wild boar makes use of food resources depending on their seasonal availability in the environment. As seen in other studies where wild boars are exotic, this species shows seasonal selection of forage, with seasonality being largely determined by food availability (Baber and Coblentz 1987; Wood and Roark 1980). Seasonal differences in diets reflected changes in availability or phenology of plants, often influenced by precipitation. In the Monte Desert, the productivity is limited by water, which controls the vegetative growth of most woody species and the germination of annual herbs and grasses (Rundel et al. 2007). Therefore, the availability of fruits and annuals such as *P. cuneato-ovata*, *S. miniata*, *D. patagonicum*, *Chenopodium* sp., *Lecanophora* sp., *Verbena* sp. and *Descurainia* sp. are higher during the wet season. Abrupt shifts in seasonal utilization of available forage, particularly in semi-arid habitats, are common (Baber and Coblentz 1987).

Regarding the selection of consumed items, wild boars selected herbs in both seasons. Herbs such as *P. cuneato-ovata*, *S. miniata* and fruits of *P. flexuosa* were the most consumed food items. Nutritional analysis of leaves of *P. cuneato-ovata* and *S. miniata* indicated that these species are a very good fodder (forage value = outstanding and exceptional, respectively). However, the bulbs of *P. cuneato-ovata* and fruits of *P. flexuosa* have relatively low nutritional value (low and good, respectively) due to their high carbohydrate content (Stasi and Medero 1983; Wainstein and González 1971a). Nevertheless, high carbohydrate input is considered important in the diet of an animal as it is an essential component in keeping the body in good physical condition and also for the accumulation of reserves to be used during more critical periods and/or periods of highest energy demand (Abaigar 1993). Therefore, we consider that wild boars in this desert environment select energy-rich food items.

In conclusion, the invasive wild boar makes use of food resources according to seasonal availability (i.e. higher trophic niche breadth during the wet season). Furthermore, within each season, it selects items with high forage quality (mainly *S. miniata* and *P. cuneato-ovata*) and high carbohydrate content, such as bulbs of *P. cuneato-ovata* and fruits of *P. flexuosa*. These resources represent immediate energy for the body. We suggest that the wild boar survival in the rather extreme environmental conditions of the Monte Desert (i.e. a prolonged annual dry period and low productivity) depends on a foraging strategy which maximizes energy intake through selected food items.

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