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María L. Reus^a, Flavio M. Cappa^a, Natalia Andino^a, Valeria E. Campos^a, Claudia de los Ríos^a & Claudia M. Campos^{ab}

^a Interacciones Biológicas del Desierto (INTERBIODES), Departamento de Biología y Museo de Ciencias Naturales, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Argentina

^b Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA-CONICET), CCT-Mendoza, Mendoza, Argentina

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ORIGINAL ARTICLE

Trophic interactions between the native guanaco (*Lama guanicoe*) and the exotic donkey (*Equus asinus*) in the hyper-arid Monte desert (Ischigualasto Park, Argentina)

María L. Reus^{a*}, Flavio M. Cappa^a, Natalia Andino^a, Valeria E. Campos^a, Claudia de los Ríos^a & Claudia M. Campos^{a,b}

^a*Interacciones Biológicas del Desierto (INTERBIODES), Departamento de Biología y Museo de Ciencias Naturales, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Argentina;* ^b*Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA-CONICET), CCT-Mendoza, Mendoza, Argentina*

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Exotic herbivores have detrimental effects on the ecosystems where they are introduced, at the level of plant communities and ecosystem processes. The native guanaco *Lama guanicoe* and the exotic feral donkey *Equus asinus* coexist in Ischigualasto Provincial Park. We quantified food availability in a plant community in the park during the wet and dry seasons, analyzed diet composition of both herbivores (by microhistological analysis of feces), and assessed the relationship between diet and plant availability and the overlap between donkey and guanaco diets. In both seasons, shrub species represented the most abundant cover type in the area, whereas grasses were the lowest plant cover during the wet season and almost non-existent in the dry season. The diet of the exotic donkey showed a high intake of grasses, and the trophic niche breadth did not change along the year. The guanaco's diet was based on the most abundant food resources (shrubs), which constituted at least 60% of the diet; it was less diverse during the dry season. The diets of donkey and guanaco showed high overlap during the dry season. We can assume, at least during the dry season, the existence of a potential competition between guanaco and donkey, which may be higher if the donkey density increases.

Keywords: diet; dryland; selectivity; trophic overlap; ungulates; Argentina

Introduction

The introduction of exotic species represents one of the three greatest threats to global biodiversity, together with climate change and habitat loss (Nuñez et al. 2010). In particular, exotic herbivores have detrimental effects on the ecosystems in which they are introduced, at the level of plant communities and ecosystem processes (see review in Vazquez 2002).

There is evidence around the world of relationships between exotic species and native ungulates and associated conservation issues (e.g. Fritz et al. 1996; Prins 2000; Frid 2001; Mishra et al. 2004; Coe et al. 2005; Vila et al. 2008; Carusi et al. 2009). In South America, some studies have analyzed the relationships between livestock (e.g. cattle and donkeys) and wild camelids, such as guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*). Overall, they found an overlap in the use of food resources (Bonino & Pelliza Sbriller 1991; Baldi et al. 2001, 2004; Puig et al. 2001; Borgnia et al. 2008). In areas of coexistence, native large mammals appear to be subordinate to the livestock with which they coexist by adapting to suboptimal habitats, while livestock concentrate on the richest ones (Borgnia et al. 2008).

In Argentina, the guanaco has become scarce throughout its distribution range, which currently represents only 40% of the original range (Cajal 1991; Franklin et al. 1997). The causes of this decline have not been well documented but they may include hunting, competition with domestic livestock and other exotic herbivores, and habitat loss resulting from agricultural development (Cunazza et al. 1995). Even so, the biggest populations occur in Patagonia and some relict and isolated populations remain in restricted areas in north-central Argentina (Sosa & Sarasola 2005; De Lamo 2011). Only 3% of the present distribution of the guanaco occurs within protected areas (Cajal 1991).

The Ischigualasto Provincial Park and World Heritage Site is a reserve located in the Monte Desert, the most arid ecoregion in Argentina (Fernández & Busso 1999). This park, together with Talampaya National Park and Sierras de Las Quijadas, protects populations of guanaco inhabiting temperate deserts. The density of the population occurring in Ischigualasto falls within the range of other populations, differing between the wet (0.10–0.12 individuals km⁻²) and dry seasons (0.6–0.75 individuals km⁻²; Acebes,

*Corresponding author. Email: reusster@gmail.com

Traba, Malo, et al. 2010), and it has been categorized as “highest priority” for conservation (Acosta & Murua 1999). In this park, like in other protected areas of Argentina (Talampaya National Park, Los Cardones National Park, and Laguna Blanca Reserve), populations of feral donkeys are also present. The guanaco occupies a great number of habitats in the Park and it has been argued that the apparent lack of displacement of guanaco by exotic herbivores could be because the native mammal uses almost exclusively some habitats and shares only part of them with exotic herbivores (Ovejero et al. 2011). Even though spatial interference between species has not been found, guanaco abundance can be affected by donkey presence (Acebes et al. 2012).

The guanaco is considered a “grazer-browser” because it is an intermediate feeder that can alternate between the use of grasses and shrubs (Puig et al. 2001). In northern Patagonia and Tierra del Fuego the diet of guanacos is composed mainly of grasses, forbs, and tree seedlings and saplings, whereas phanerophytic shrubs are avoided (Raedeke 1980; Bonino & Pelliza Sbriller 1991; Puig et al. 1996, 1997, 2011; Soler et al. 2013). Nevertheless, when the availability of herbaceous strata decreases during winter, a dietary shift from grazing to browsing was observed in some guanaco populations (Raedeke 1980; Bahamonde et al. 1986; Bonino & Pelliza Sbriller 1991; Puig et al. 1996). This flexibility to change diet according to food availability extends to the consumption of lichens and cacti in the arid coast of the Atacama Desert (Raedeke & Simonetti 1988) and the tree leaves of the deciduous Magellanic forest (Martínez-Pastur et al. 1999; Cuevas 2002; Cavieres & Fajardo 2005). Whereas in north-central Chile the guanaco’s trophic niche breadth is wider during the dry season (Cortés et al. 2003), in habitats of the Magellanic forest-steppe ecotone, southern Puna, and Patagonia the guanaco uses a wide array of food resources and expands its trophic niche when resources are more abundant (Raedeke 1980; Cajal 1989; Puig et al. 1996, 2011).

Like guanacos, donkeys can alternate between browsing and grazing (e.g. Fowler de Neira & Johnson 1985; Grinder et al. 2006). As hindgut-fermenting equids, donkeys spend a lot of time foraging, and their feeding strategy is based on high intake of food with low attainment of nutrients, mainly in ecosystems with homogeneous resource distribution (for example, grasslands). However, donkeys retain food longer in the digestive tract and digest fiber more efficiently than do the other equids and, in that sense, donkeys are more “ruminant-like” (Pearson et al. 2001). Although some authors have considered that donkeys behave

predominantly as browsers and are highly opportunistic in their diet (Woodward & Ohmart 1976; Grinder et al. 2006), most studies report that they select to consume grasses and graminoids, making browsing less important or secondary to grazing (Cosyns et al. 2001; Smith & Pearson 2005 and references therein). Because of the low energy costs of walking, long foraging times per day and the ability to tolerate thirst, donkeys have access to under-utilized sources of forage that are inaccessible to other herbivores such as cattle (Mueller et al. 1998; Smith 1999; Smith & Pearson 2005).

Considering that the guanaco is a herbivore with a long evolutionary history in arid and semiarid ecosystems of Argentina, we can expect that the native species is better adapted to the food resources provided by the environment than the relatively recently arrived donkey (Bailey & Schweitzer 2010). Nevertheless, the donkey is probably a good ecological equivalent and potential competitor because of its adaptations to living in arid environments (Novillo & Ojeda 2008). With the aim of elucidating how these herbivores use food resources in an arid ecosystem, we quantified food availability in a plant community of Ischigualasto Park during the wet and dry seasons, and analyzed the diet composition of both herbivores. Also, we assessed the relationship between diets and plant availability and the dietary relationships between the donkey and the guanaco.

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 1300 m asl, and is included in the northern Monte desert (Burkart et al. 1999). The climate is arid, with an average annual precipitation of 183 mm. It is characterized by humid summers (average precipitation November–March: 100 mm) and dry winters (average precipitation April–October: 8 mm). 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 scrublands dominated by shrubs, cacti, and bromeliads (Márquez et al. 2005; Acebes, Traba, Peco, et al. 2010).

Vegetation sampling and collection of feces were performed in the Los Colorados Formation, which includes the community of *Zuccagnia punctata* (Fabaceae) described by Márquez et al. (2005). Mean plant cover of this community is 15%, dominated by

Z. punctata accompanied by *Atriplex spegazzini* and *A. lithophila* (Chenopodiaceae). The vegetation has strong edaphic constraints as it grows on soils composed of Triassic sandstone with high salt content. Two predominant plant associations can be distinguished: communities associated to watercourses and to the upper belt. The former contains species such as *Juncus acutus* (Juncaceae), *Tessaria dodonaefolia*, *T. absinthioides*, and *Baccharis salicifolia* (Asteraceae), *Sporobolus rigens* and *Distichlis scoparia* (Poaceae). In the upper belt there occur coppice stands of *Ramorinoa giroiae*, and *Z. punctata* (Fabaceae), *A. spegazzini*, and *Suaeda divaricata* (Chenopodiaceae), *Lycium ciliatum* (Solanaceae), *Capparis atamisquea* (Capparaceae), *Tillandsia* spp. (Bromeliaceae), and *Echinopsis leucantha* (Cactaceae) (Cortez et al. 2005). Work was conducted in an area of approximately 5 ha, where presence of guanacos and donkeys was confirmed from tracks, fresh feces, cuts in plants and trails.

Food availability

The supply of plant species was recorded during the dry season (April–November 2005) and the wet season (December 2005–March 2006), considering vegetation cover as an estimation of food availability. Plots were randomly selected across the study area (17 in the wet season and 10 in the dry season = 27 plots), 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 quadrats of 2×2 m, through the projection of the exposed leaf area on the ground. The first quadrat was located at the intersection of the lines and the other 12 were 2 m apart on the lines, giving a total sampling area of 52 m^2 per plot.

Diet composition

Samples of fresh feces were collected in order to estimate the use of food resources. Guanaco feces were taken from different communal “defecating sites”. The samples of donkey dung consisted of amounts of approximately 50 g of dung from different depositions located at least 20 m apart. Collected samples (guanaco: wet season $N = 14$, dry season $N = 11$; donkey: wet season $N = 7$, dry season $N = 12$) were analyzed by microhistological analysis of feces following the method by Dacar and Giannoni (2001) in order to determine diet composition. Fecal samples were macerated in a solution of 17.5% NaHCO_3 for about 24 hours. The material was rinsed with tap water and sieved through a metal screen with openings of $74 \mu\text{m}$. Three microscope slides were prepared from each sample. Fifty

microscope fields were systematically examined on each slide under a microscope at $400\times$ magnification, totaling 150 fields per sample. Histological features of leaf epidermis 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 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 (Holechek & Gross 1982).

The potential bias associated with the microhistological analysis of feces as an estimate of herbivore diet composition has been discussed (e.g. Vavra & Holechek 1980; Holechek 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, cacti, and bromeliads. We used Kruskal–Wallis ANOVA and the post-hoc pairwise Wilcoxon test with Holm correction ($p < 0.05$) 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 diet.

Diet selection was assessed using Bonferroni simultaneous confidence intervals (Neu et al. 1974; Byers et al. 1984) for plant species having a percentage of occurrence in diets equal to or more than 0.5%. These intervals determine the proportion of use for each plant species and compare it to the expected proportion (P_e = 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, respectively.

The Shannon–Weaver index of ecological diversity (Colwell & Futuyma 1971) was estimated as an indicator of trophic niche breadth, that is, a measure of diversity of plant species and their percentage of occurrence in the diet ($H' = -\sum p_j \log p_j$, where: $p_j = n_j/N$ is the proportion of the total number of plants of the species j , n_j = number of plants of the

species j , and N = total number of plants). The Mann–Whitney non-parametric test was used to determine whether there were significant differences between herbivores and seasons, considering each fecal sample as sampling unit.

In order to assess an association based on similarity among diets, a redundancy analysis (RDA) was applied to the matrix of percentage of occurrence of plant species in the diets, including only species that appeared in at least five samples (response variables). This constrained ordination was performed because datasets had a short gradient ($L = 2.69$) indicating linear response curves, and explanatory variables were in the form of categorical predictors (Ter Braak & Smilauer 2002). The association of each herbivore (guanaco and donkey) 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. Dietary overlap of all identified items was estimated with Pianka's (1986) index: $O = (\sum pij \sum pik) / (\sum pij^2 \sum pik^2)^{1/2}$, where O is the degree of overlap between the species j and k , and p_{ij} and p_{ik} 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.

Analysis was carried out using RStudio statistical software version 0.95.265 (Free Software Foundation, Inc. 2009–2011; <http://www.rstudio.org/>).

Results

Food availability

Mean total plant cover in Los Colorados Formation was 16.6% during the wet season (27 plant species) and 14.6% in the dry season (20 plant species). Both seasons showed significant differences in plant cover among functional groups (Kruskal–Wallis, wet season: chi square = 69.51, $p < 0.00001$, $df = 5$; dry season: chi square = 33.31, $p < 0.00001$, $df = 5$). In both seasons, shrubs were the most abundant cover

type. Grasses were the lowest plant cover during the wet season and non-existent in the dry season. Annual forbs were not detected in either season (Figure 1). The most representative species (with $\geq 1\%$ of plant cover) were *R. girolae*, *Z. punctata*, *Atriplex* sp., *Prosopis torquata*, and *Opuntia* sp.

Diet composition

The items identified in both herbivores' diets were mainly leaves; the only fruits recorded were from *P. torquata* (Table 1). The composition of the guanacos' diet based on functional groups was significantly different in both seasons (Kruskal–Wallis, wet season: chi square = 52.06, $p < 0.00001$, $df = 5$; dry season: chi square = 47.86, $p < 0.00001$, $df = 5$). The guanacos' diet was composed of 11 food items in the wet season and 10 food items in the dry season, and the main food functional group included in the diet was shrubs. Grasses, bromeliads, and cacti were the next most common functional groups (Figure 1).

The composition of the donkeys' diet based on functional groups was significantly different in both seasons (Kruskal–Wallis, wet season: chi square = 18.09, $p = 0.0028$, $df = 5$; dry season: chi square = 43.46, $p < 0.00001$, $df = 5$). The donkeys' diet was composed of 17 food items in the wet season and 21 food items in the dry season. During the wet season the most consumed group was grasses, whereas in the dry season the main groups consumed by donkeys were grasses and shrubs (Figure 1).

Diet selection and trophic niche breadth

In the wet season, the guanacos selected species such as *Z. punctata*, *Capparis atamisquea*, and *P. torquata*. During the dry season, the most common items among those selected by guanacos were *Cyclolepis genistoides*, *Trichomania usillo*, grasses, *Tephrocactus* sp., and *Tillandsia* sp. (Table 2).

During the wet season, the donkeys selected grasses, the shrub *C. genistoides*, and the bromeliad *Deuterocohnia longipetala*. In the dry season, as well as the grasses and the shrub *C. genistoides* selected in the wet season, the donkeys added *Prosopis chilensis*, *T. usillo*, *Solanum eleagnifolium*, and *Tillandsia* sp. (Table 2).

Figure 1. Comparison between food availability (cover of plant species) and diets (relative percentage of occurrence of plant species) of donkey (*Equus asinus*) and guanaco (*Lama guanicoe*) in the wet and the dry seasons taking into account (A) the less common plant functional groups: annual forbs, bromeliads, cacti and trees; and (B) the most common plant functional groups: grasses and shrubs. 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 dataset, respectively. The ends of the vertical lines indicate the minimum and maximum data values; the points outside the ends of the whiskers are outliers.

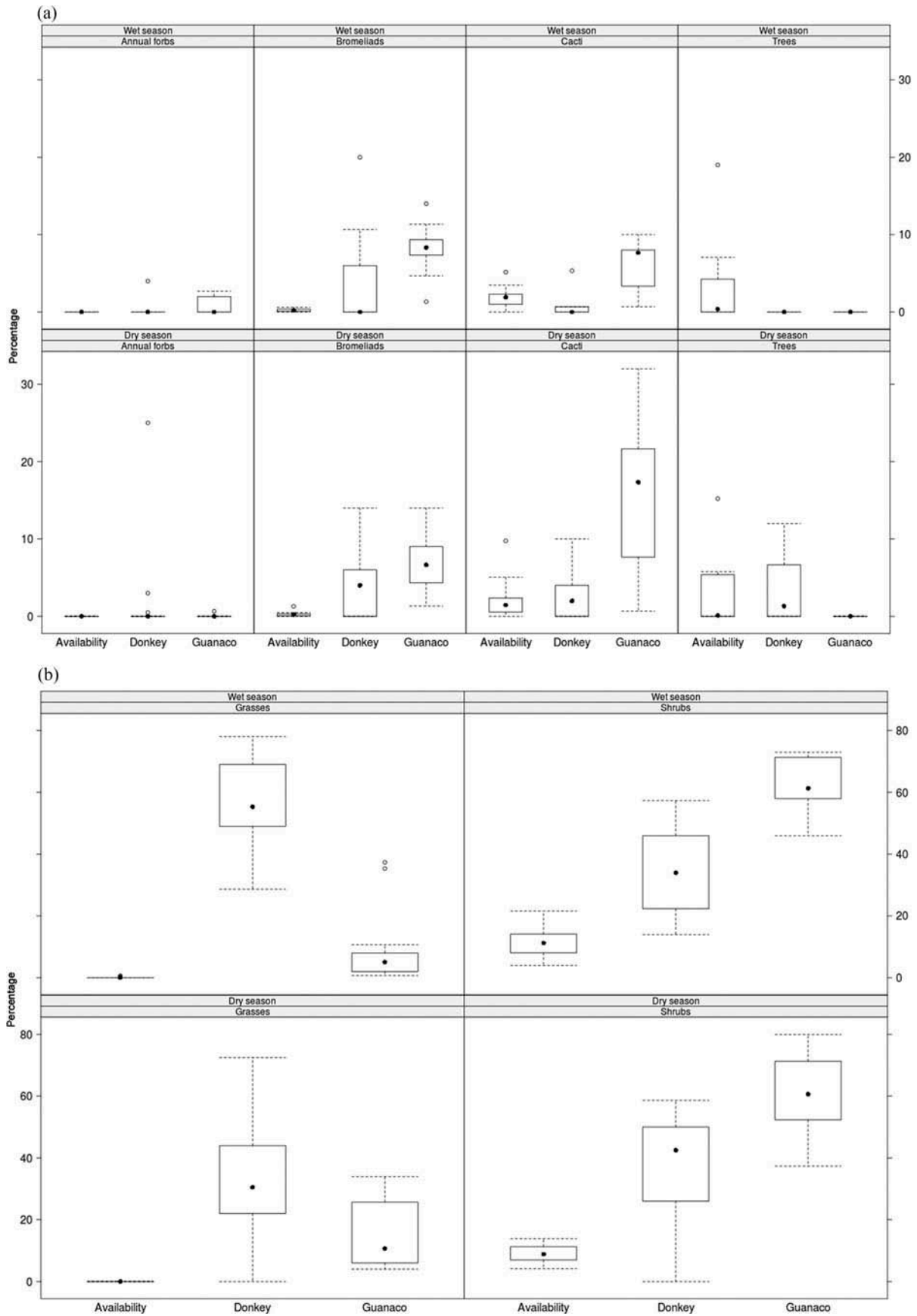


Table 1. Composition of diets (mean \pm SE of relative percentage of occurrence of plant species) of guanaco (*Lama guanicoe*) and donkey (*Equus asinus*) during wet and the dry seasons in the Ischigualasto Provincial Park (San Juan, Argentina).

	Acr	Wet season		Dry season	
		Guanaco	Donkey	Guanaco	Donkey
		<i>n</i> = 14	<i>n</i> = 7	<i>n</i> = 11	<i>n</i> = 12
<i>Prosopis chilensis</i>		—	—	—	1.23 \pm 0.70
<i>Prosopis flexuosa</i>		—	—	—	1.23 \pm 0.43
Total trees		—	—	—	2.46
<i>Atriplex</i> sp.	(atrip)	—	5.42 \pm 1.29	—	7.28 \pm 1.75
<i>Bougainvillea</i> sp.	(bouga)	1.71 \pm 0.39	—	0.66 \pm 0.30	—
<i>Capparis atamisquea</i>	(catam)	15.28 \pm 2.23	—	1.82 \pm 1.00	—
<i>Cyclolepis genistoides</i>	(cgenis)	3.19 \pm 0.87	10.57 \pm 3.97	21.03 \pm 1.82	14.55 \pm 3.04
<i>Larrea</i> sp.	(larrea)	—	1.42 \pm 0.42	—	3.32 \pm 1.54
<i>Lycium</i> sp.		—	0.67 \pm 0.48	—	1.02 \pm 0.31
<i>Prosopis torquata</i> (fruit)		—	2.29 \pm 2.29	—	—
<i>Prosopis torquata</i>	(ptorq)	11.33 \pm 1.50	8.38 \pm 2.31	2.97 \pm 0.86	4.64 \pm 2.58
<i>Trichomania usillo</i>	(tusil)	8.24 \pm 2.24	—	20.36 \pm 5.82	3.08 \pm 1.77
<i>Zuccagnia punctata</i>	(zpunc)	22.50 \pm 2.73	4.19 \pm 1.20	12.84 \pm 1.85	4.18 \pm 0.88
Total shrubs		62.25	32.94	59.68	38.07
<i>Solanum eleagnifolium</i>		0.76 \pm 0.27	0.50 \pm 0.50	—	2.19 \pm 1.91
Total annual forbs		0.76	0.50	—	2.19
<i>Aristida</i> sp.		—	6.19 \pm 2.49	—	7.70 \pm 3.35
<i>Cortaderia</i> sp.		—	—	—	0.79 \pm 0.47
<i>Distichlis spicata</i>		—	20.38 \pm 4.77	—	6.19 \pm 1.43
<i>Pappophorum</i> sp.		—	6.86 \pm 1.85	—	5.44 \pm 1.88
<i>Sporobolus rigens</i>		—	1.24 \pm 1.13	—	1.95 \pm 1.34
<i>Trichloris crinita</i>		—	20.00 \pm 4.00	—	9.77 \pm 2.14
Undetermined grass		8.52 \pm 3.19	2.09 \pm 1.13	16.24 \pm 3.52	1.31 \pm 0.49
Total grasses	(grass)	8.52	56.76	16.24	33.15
<i>Opuntia</i> sp.		—	0.86 \pm 0.75	—	0.82 \pm 0.44
<i>Tephrocactus</i> sp.	(tephr)	5.62 \pm 0.77	—	14.18 \pm 2.75	1.55 \pm 0.83
Total cacti		5.62	0.86	14.18	2.37
<i>Deuterocohnia longipetala</i>		—	6.47 \pm 5.72	—	—
<i>Tillandsia</i> sp.	(tilla)	8.19 \pm 0.82	1.05 \pm 1.05	6.84 \pm 1.25	3.73 \pm 1.07
Total bromeliads		8.19	7.52	6.84	3.73
Undetermined dicot		8.42 \pm 0.89	—	1.46 \pm 0.35	2.45 \pm 0.71

Notes: Only plant species with percentages \geq 0.5% were included; *n* is the number of fecal samples. The acronym (Acr) of the species used in redundancy analysis (RDA, Figure 2) is given.

The guanacos' diet was significantly more diverse than the donkeys' diet during the wet season ($W = 35$, $p = 0.00170$; dry season: $W = 131.5$, $p = 0.97$). While the donkey's diet retained its diversity in plant composition through the year ($W = 48$, $p = 0.07$; Shannon index value, wet season = 1.24 and dry season = 1.64), the diversity of the guanaco's diet decreased significantly during the dry season ($W = 101.5$, $p = 0.022$; Shannon index value, wet season = 1.84 and dry season = 1.69).

Dietary relationships

The RDA of diet data showed correlation between diet and the explanatory variable ($R^2 = 0.47$, $F_3 = 13.72$, $p = 0.005$) for the first three axes. The first, second, and third axes explained 28% ($F_1 = 31.50$, $p = 0.001$), 13.5% ($F_1 = 8.73$, $p = 0.001$), and 3% ($F_1 = 0.92$, $p = 0.44$) of

the total variability, respectively (Figure 2). The guanacos' diets during the wet and dry seasons were closely associated with shrubs (such as *C. atamisquea*, *Z. punctata*, *Bougainvillea* sp., and *T. usillo*), the bromeliad *Tillandsia* sp., and the cactus *Tephrocactus* sp., while the donkeys' diets were associated with grasses, *Larrea* sp., and *Atriplex* sp. Both herbivores shared the consumption of *C. genistoides* in the dry season and *P. torquata* in the wet season (Figure 2). The diets of donkeys and guanacos showed low overlap during the wet season ($O = 0.36$), but overlap increased during the dry season ($O = 0.68$).

Discussion

Both herbivores can be considered consumers with mixed feeding because they used grasses (the item mainly consumed by grazers) and shrubs (one of the

Table 2. Plant species selected (S), avoided (A), or used indifferently (I) by guanaco (*Lama guanicoe*) and donkey (*Equus asinus*) during wet and dry seasons in the Ischigualasto Provincial Park (San Juan, Argentina).

	Wet season					Dry season				
	Pe	Bonferroni confidence intervals		Pe		Bonferroni confidence intervals				
		Guanaco	Donkey			Guanaco	Donkey			
TREES										
<i>Prosopis chilensis</i>	—	—	—	0.0000	—	(0.00440–0.02528)	S			
<i>Prosopis flexuosa</i>	—	—	—	0.0158	—	(0.00477–0.02607)	I			
SHRUBS										
<i>Artiplex</i> sp.	0.1120	—	(0.02990–0.08059)	A	0.0777	—	(0.06186–0.11031)	I		
<i>Bougainvillea</i> sp.	0.0000	(0.00947–0.03155)	S	—	0.0000	(–0.00032–0.01408)	I	—		
<i>Capparis atamisquea</i>	0.0019	(0.15040–0.21028)	S	—	0.0000	(0.00679–0.03031)	S	—		
<i>Cyclolepis genistoides</i>	0.0090	(0.02183–0.05100)	S	(0.07290–0.14155)	S	0.0336	(0.17968–0.25135)	S	(0.13913–0.20427)	S
<i>Larrea</i> sp.	0.0771	—	(0.001128–0.02747)	A	0.0169	—	(0.02052–0.05303)	I		
<i>Lycium</i> sp.	0.0544	—	(–0.00218–0.01654)	A	0.0807	—	(0.00248–0.02114)	A		
<i>Prosopis torquata</i>	0.0811	(0.10409–0.15652)	S	(0.05542–0.117837)	I	0.1455	(0.01548–0.04543)	A	(0.03538–0.07478)	A
<i>Trichomania usillo</i>	0.0103	(0.06984–0.11494)	S	—	0.0000	(0.17259–0.24333)	S	(0.02148–0.05449)	S	
<i>Zuccagnia punctata</i>	0.1834	(0.23068–0.29943)	S	(0.01966–0.06411)	A	0.1412	(0.10282–0.16188)	I	(0.03184–0.06977)	A
ANNUAL FORBS										
<i>Solanum eleagnifolium</i>	0.0000	(0.00171–0.01650)	S	(–0.00281–0.01287)	I	0.0000	—	(0.01111–0.03778)	S	
GRASSES	0.0053	(0.07442–0.12063)	S	(0.51900–0.62880)	S	0.0000	(0.13453–0.19955)	S	(0.36066–0.44537)	S
CACTI										
<i>Opuntia</i> sp.	0.0629	—	(–0.00161–0.01895)	A	0.0800	—	(0.00157–0.01900)	A		
<i>Tephrocactus</i> sp.	0.0111	(0.04675–0.08544)	S	—	0.0660	(0.11517–0.17671)	S	(0.00662–0.02967)	A	
BROMELIADS										
<i>Tillandsia</i> sp.	0.0159	(0.07245–0.11819)	S	(–0.00027–0.02080)	I	0.0167	(0.04808–0.09267)	S	(0.02812–0.06440)	S
<i>Deuterocohnia longipetala</i>	0.0000	—	(0.00331–0.08550)	S	—	—	—	—		

Notes: Data in parentheses are Bonferroni confidence intervals; Pe is the expected proportion (relative plant cover in the field). Only plant species with percentages $\geq 0.5\%$ were included.

items consumed by browsers; Hoffmann & Stewart 1972). However, in the community of Los Colorados in the Ischigualasto Provincial Park, guanacos showed a strong tendency to be browsers, while donkeys behaved as grazers.

Diet composition, diet selection, and trophic niche breadth

Previous studies showed the capability of guanacos to change diet according to food availability (Raedeke 1980; Bonino & Pelliza Sbriller 1991; Puig et al. 1996, 1997, 2001, 2011). Only one study carried out in La Payunia Reserve (Patagonia) showed that shrubs were the primarily consumed item (67%) throughout the year, whereas grasses represented 26% of the diet (Candia & Dalmaso 1995). Similar to the results of that study, we did not find a high consumption of grasses; indeed, shrubs were highly consumed while grasses and cacti were incorporated mostly during the

dry season (almost 30% of the diet). As was previously observed in the study area, the addition of cacti to the diet is a strategy that could improve water intake during periods when free water or green vegetation is not available (Malo et al. 2011). This capability of guanacos to utilize different food resources could reflect a plastic and flexible response to environmental conditions, with more or less abundance of food resources and important variations in quality along time (Puig et al. 1996).

In Ischigualasto Provincial Park, the wider trophic niche breadth of guanacos in the wet season can be interpreted as an adaptation to arid and semiarid environments, where high climate fluctuations reduce the predictability of phenological and nutritional changes in the vegetation and herbivores develop a “cafeteria style” (Hansen et al. 1985), continually sampling the available forages to assess the species quality (Goss-Custard 1981). This result may agree with the selective quality hypothesis (Weckerly &

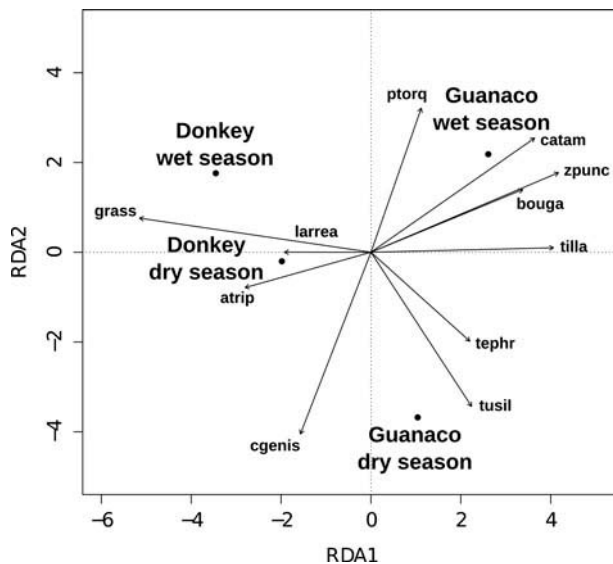


Figure 2. Redundancy analysis (RDA) biplot of plant species in the diet and explanatory parameters (herbivores: guanaco and donkey, and seasons: wet and dry). For abbreviations of plant species see Table 1. In the biplot plant species in the diets were represented by arrows and explanatory parameters were 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.

Kennedy 1992), in which it is expected that animals are less selective (high dietary diversity, wide trophic niche breadth) during periods of higher resource abundance because high-quality food resources are in greater supply and more homogeneously distributed. Instead, during the dry season the guanaco showed a narrower trophic niche, which could imply that the herbivore included fewer but more nutritious plants in its diets. Foraging behavior and digestive adaptations to harsh environments have allowed the guanaco to become the dominant large herbivore of the scrubland and steppes of South America (González et al. 2006).

Similar to previous studies showing that donkeys select grasses and graminoids for consumption (Cosyns et al. 2001; Smith & Pearson 2005 and references therein), our results also showed that consumption of grasses by donkeys was significantly higher than the environmental availability of grasses, which implies search and selection of this food item. At our study site, the most common grasses in the donkey's diet, such as *D. spicata* and *T. crinita*, were scarce in both seasons and they usually grew under shrubs or close to water bodies on saline soils. In semi-natural

conditions in European ecosystems, Van Assche (1993) reported that when grasses became very scarce, donkeys caused a huge impact on other species, such as woody plants. This was also observed in the hyper-arid Monte region where donkeys consumed and damaged trunks of *Trichocereus terscheckii*, affecting the reproductive parameters of this columnar cactus (Malo et al. 2011; Peco et al. 2011).

Dietary relationships

Our results showed a higher diet overlap between guanacos and donkeys in the dry season and a lower overlap during the wet season. Previously, also in Patagonia, high diet overlap between guanacos and freely grazing horses was found (Puig et al. 2001). Competition for food between domestic animals and herbivorous wildlife species varies over time and space as a function of demand relative to the quantity and quality of available forage (Barnes et al. 1991). Even though in our study site guanaco and donkey co-occurrence does not show evidence of spatial overlap, maybe due to the low density of guanacos and the even lower densities of donkeys (Ovejero et al. 2011; Acebes et al. 2012), the high trophic overlap during the dry season suggests the existence of a potential trophic competition between guanacos and donkeys, that likely increases if the density of donkeys becomes higher, especially during the season when food resources are scarce. These results are important for the management of drylands of South America, where populations of threatened herbivorous species, such as guanacos, coexist with domestic animals, sharing spatial and trophic resources, even in protected areas.

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