



Guanaco's diet and forage preferences in *Nothofagus* forest environments of Tierra del Fuego, Argentina

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Abstract

Aim of study: Guanaco (*Lama guanicoe* Müller), is a South American native ungulate widely distributed in Patagonia, which in the island of Tierra del Fuego (TF), extends its habitat into *Nothofagus* spp. forests. Within these forests, guanacos consume lenga (*Nothofagus pumilio*) leaves and twigs, and other understory species. The aim of this work was to determine: 1) the spring and summer diet of free ranging guanacos, and 2) which plants, grown in the forest understory, guanacos do prefer, or avoid, in these seasons of great forage abundance.

Area of study: Tierra del Fuego (Argentina), on three representative areas which combined *Nothofagus* forests and adjacent meadows (vegas).

Material and Methods: Guanacos' diet was determined by comparing epidermal and non-epidermal plant fragments with micro-histological analyses of feces. The analysis was made from composite samples of fresh feces, collected at the seasons of maximum forage productivity (spring and summer).

Main results: During spring, 48% of guanacos' diet was composed of lenga leaves, 30% of grass-like species, 15% of grasses, and less than 7% of herbs, shrubs, and lichens. In summer, 40% of the diet was composed of grasses, 30% of lenga leaves, 25% of grass-like species and the rest corresponded to herbs, shrubs, and lichens. Within the forest understory, guanaco selected lenga leaves and twigs, grass species were consumed according to their availability (or sometimes rejected), while other herbs were not consumed at all.

Research highlights: Guanacos' consumption preference for lenga, even considering the high availability of other forages, could adversely affect forest regeneration.

Keyword: feces analysis; forest sustainability; forest understory; micro-histological analyses; Patagonia.

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Introduction

Large herbivores' diet is often limited by the quantity and quality of available forage, and also by their intrinsic anatomical adaptations that facilitate feeding (McNaughton, 1986). These facts make herbivores to select grazing areas of abundant and nutritionally good forage quality (Pelliza Sbriller *et al.*, 1997). According to its feeding habits, guanaco (*Lama guanicoe* Müller), a native ungulate widely distributed in South America, may be considered a generalist of intermediate selectivity, since its diet include most of the plants present in its natural habitat (Baldi *et al.*, 2004).

Guanaco is the largest native ungulate that inhabits Patagonia, the region that covers the southern tip of South America in Argentina and Chile. In Argentina, this region comprises different physiographic environments, from arid and semiarid plateaus in the east, steppe-forest ecotone in the piedmont of the Andes going west, to dense *Nothofagus* spp. forests at higher altitudes of the Andean cordillera. In continental Patagonia, guanaco's habitat includes arid and semiarid grassland steppes and shrublands, and open ranges in the forest-steppe ecotone (Franklin, 1982; Baldi *et al.*, 1997), but excludes denser forest areas dominated by *Nothofagus* spp. or by other tree species. In the

southern island of Tierra del Fuego (TF), instead, guanacos' habitat includes *Nothofagus* spp. forests and adjacent meadow areas (Bonino & Fernández, 1994; Montes *et al.*, 2000). One of the possible reasons for the expansion of guanacos' habitat into *Nothofagus* forests is that the puma (*Felis concolor*), the main predator of guanaco in continental Patagonia, has not been yet recorded in this island. In TF, *Nothofagus* spp. forests grow at low altitude, and their physiography present a matrix of forest embedded of open wetlands (meadows), located in depressions of the landscape. These meadows, regionally named “*vegas*”, although highly overgrazed in the past, are sites of high potential productivity, mainly provided by tender species of the Cyperaceae, Juncaceae, and Poaceae families, which in general supply excellent forage quality (Cassola, 1988). In continental Patagonia, guanacos' diet mainly consists of grasses, grass-like, herbs, and shrub species (Puig *et al.*, 2011). In the southern area of guanaco's distribution in TF, and in spite of the availability of tender herbs and grasses in the *vegas*, the consumption of lenga beech leaves [*Nothofagus pumilio* (Poepp. & Endl.) Krasser], and to a lesser extent of ñire [(*Nothofagus antarctica* (G. Forst.) Oerst.) and several other low abundant shrubs, seems to constitute an important part of its diet all year round (Raedeke, 1980; Bonino & Pelliza Sbriller, 1991; Soler Esteban *et al.*, 2011; Muñoz & Simonetti, 2013).

The forest environments dominated by lenga trees in TF are considered of great ecological, economic, and landscape value (Bava & Rechene, 2004; González *et al.*, 2006b). While the understory of these forests usually presents lower vegetation cover as compared to *vegas* (Boelcke, 1957), and guanaco seems to prefer these *vegas* for feeding purposes (Bank *et al.*, 2003; Clausen *et al.*, 2006; Puig *et al.*, 2011), evidences show that it also feeds on lenga beech saplings and on some shrub species (Soler Esteban *et al.*, 2011). *Vegas* are critical habitats for guanacos during the breeding season, allowing increased reproductive success as compared to other habitats (Bank *et al.*, 2003; Wursten *et al.*, 2013). On the other hand, while lenga beech saplings may be an important component of the guanacos' diet, the negative effects of its continuous browsing and

trampling may compromise future forest development (Rebertus & Veblen, 1993; Bava & Rechene, 2004). The aim of this study was then to determine: 1) the composition of the diet of free ranging guanacos during spring and summer in three representative areas of TF which combine *vegas* and *Nothofagus* forests; and 2) which of the forage plants grown in the forest understory guanacos do prefer, or avoid, in these seasons of great food abundance. The results of this study will provide scientific information to know and compare guanacos' dietary preferences when grazing in different environments of insular and continental areas of Patagonia. Determining the incidence of *Nothofagus* spp. in guanacos' diet could also help understand its effects on lenga regeneration in TF, and provide essential information for designing management plans aimed at preserving not only guanacos' habitat, but also the sustainable growth and development of *Nothofagus* spp. forests.

Materials and methods

Study area

The study area, located in the center of Tierra del Fuego province (TF), Patagonia Argentina (54° 40' S, 67° 35' W, Figure 1), consists of three typical paddocks situated in landscapes that alternate undulated areas with valleys. One paddock was located in “Estancia María Cristina” (MC), and two in “Corazón de la Isla Reserve” (Reserve 1 and Reserve 2, R1 and R2, respectively, Figure 1 and Table 1). Their landscapes are composed of lenga beech forests with some very scattered ñire trees, surrounded by adjacent wet *vegas* in which herbs and grasses of the Cyperaceae, Juncaceae, and Poaceae families prevail. The regional climate is characterized by short, cool summers, and long, snowy, and frozen winters. Annual average wind speed outside the forests is 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms (Martínez Pastur *et al.*, 2009). Average annual temperature is 4.5 °C; annual precipitation averages 467 mm and, in the form of either rain or snow, is

Table 1. Main physiographic and stand characteristics of the study sites in Tierra del Fuego, Argentina. For altitude, slope and basal area, mean values (\pm S.E.) are presented.

Variable	María Cristina	Reserva 1	Reserva 2
Latitude	54° 28' 21.1''	54° 27' 18.0''	54° 23' 56.7''
Longitude	67° 34' 21.7''	67° 30' 32.8''	67° 13' 35.9''
Altitude (m amsl)	192	182	171
Predominant exposure	North	South	West
Slope (°)	7.7 (0.5)	13.9 (0.8)	11.9 (0.7)
Forest basal area (m ² ha ⁻¹)	56.4 (3.2)	49.7 (3.2)	42.3 (4.7)

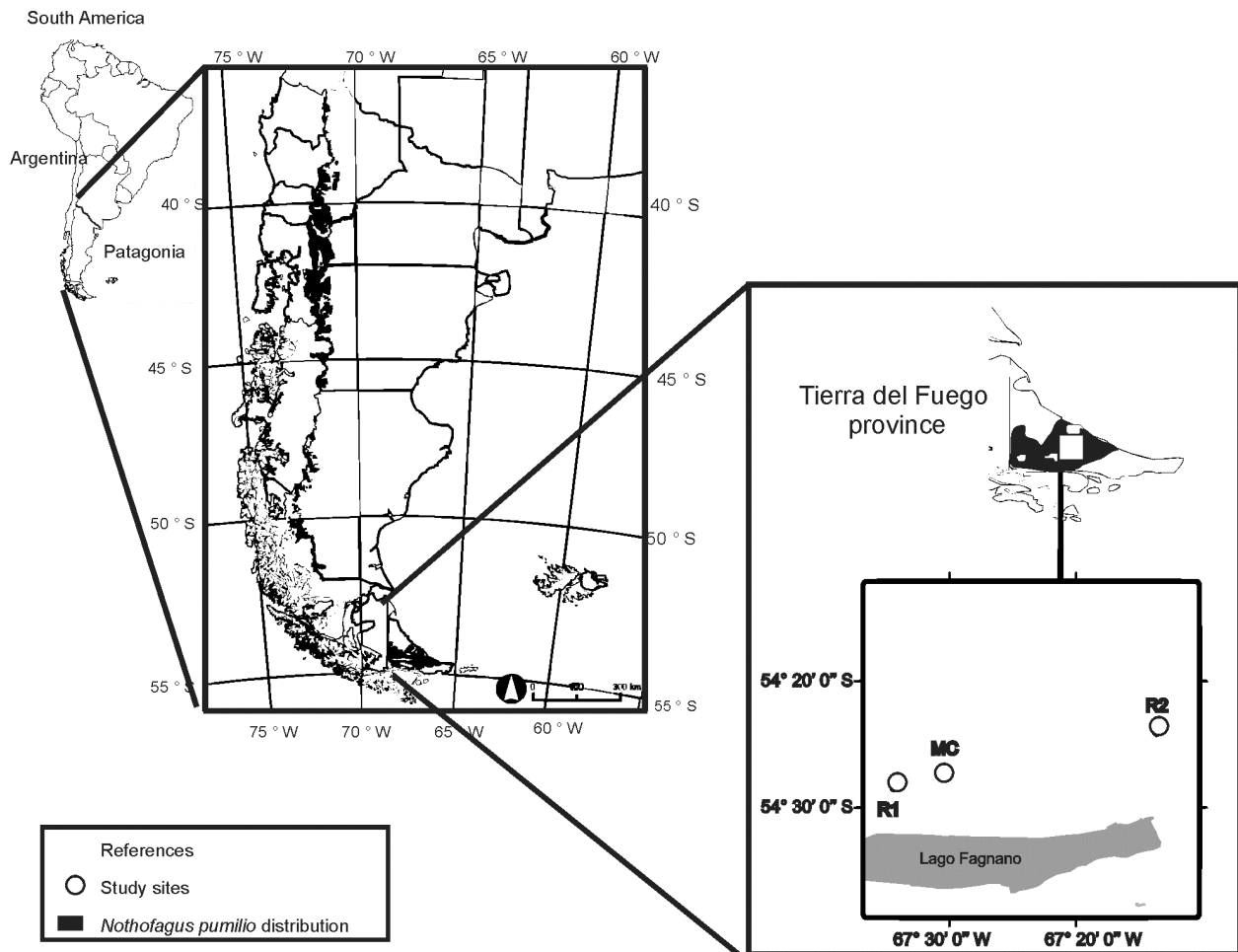


Figure 1. Location of the study sites (Estancia María Cristina: MC, Reserva Corazón de la Isla 1 (R1) y Reserva Corazón de la Isla 1 (R2)) in Tierra del Fuego province, Patagonia, Argentina.

evenly distributed along the year (Pisano, 1977). In the three paddocks, the forest had been used for more than 50 years for timber production based on selective cut of the best lenga beech trees (high-grading). At present and after livestock exclusion (at least 10 years ago), natural populations of guanaco are the only ungulates grazing in these sites.

Feces collection for determining feeding habits

In each paddock and within their respective forest area, we selected a representative sub-area (~ 15 ha) to sample guanacos' feces. Although guanacos may feed in the vegas or inside the forest, they showed a particular feces deposition behavior, concentrated in specific places within the *Nothofagus* spp. forests [named dung-piling, (Franklin, 1982)], and rarely in vegas (Soler Esteban *et al.*, 2013). In each site, fresh fecal samples (recognized because they presented a typical greenish color as compared to older feces), were collected during spring (November 2009) and summer (February 2010). Feces collection was done from five

active dung-pilings distant at least 50 m one to each other, mixed together and put in plastic bags totalizing 100 to 150 g each. Spring and summer feces were then considered as independent samples.

Botanical and fecal analyses

The botanical identification of plant tissues of reference plants collected in the three study sites was done by determining epidermal and non-epidermal plant fragments based on the micro-histological analysis method (Williams, 1969) adapted for Patagonian plants by Latour & Pelliza Sbriller (1981). At the same time of feces collection, we also sampled plants of all taxa present in either the vegas or in the forest understory. The analysis involved drying the plant material and feces at 60 °C for 48 h, milled in an analytical mill (IKA A11) until reaching particle sizes of about 1 mm, and mounted on microscope slides for further identification. This microscopic identification allowed performing species-specific patterns of plant (items) for comparison with those found in feces. Microscopic observations

of fecal samples showed different frequencies of species epidermis, so those results were expressed as percentage values of the items, at genera or species levels. Fecal samples were mounted on five microscope slides and 20 fields per slide were examined using 100 × magnifications. These analyses allowed grouping the results of these observations into six vegetation groups: trees, grasses, herbs, grass-like, shrubs, and lichens. Quantification of items composing each diet was done according to Holeček & Vavra (1981), and Holeček & Gross (1982). All analyses were conducted at the Botany laboratory, Universidad Nacional de la Patagonia “San Juan Bosco”, in Comodoro Rivadavia (Chubut, Argentina).

Biomass availability in the forest understory

To determine biomass availability in the forest understory, we placed 3 transects per paddock. The transects, 320 m long each, were located in parallel and distant about 300 m one to the other, starting from the edge of each vega toward the interior of the forest. Along each transect, 1 m² quadrats were placed at 10, 20, 40, 80, 160 and 320 m. The understory biomass inside each quadrat was cut at 2 cm aboveground, collected, separated into grasses, herbs, shrubs and trees, put in plastic bags, taken to the lab, oven-dried at 75 °C for 48 h, and weighed. Biomass was expressed as kg DM ha⁻¹, and was harvested in spring and summer simultaneously with feces collection.

Diet selectivity

Diet selection was analyzed considering aboveground biomass present in the forest understory during spring and summer, and used as an estimation of food availability. This was performed according to Ivlev's selectivity index modified by Jacobs, 1974 (Lechowicz, 1982), as:

$$D_i = (r_i - p_i) / (r_i + p_i - 2 * r_i * p_i)$$

where: r_i is the relative abundance of plant group i in the guanacos' feces, and p_i is relative abundance of that group in the field. D_i varies between -1 (strong avoidance) and 1 (strong selection), while a value near 0 indicates that the forage resource is consumed proportionally to their availability in the environment. According to Puig *et al.* (1996), the limit to determine if an item is consumed according to its availability in the environment ranges from -0.3 to 0.3. The selectivity of guanaco, by considering understory groups of grasses, herbs, shrubs and trees (lenga leaves and twigs of seedlings and saplings) per site and season, was

evaluated by relating the percentage of each group in the diet with its relative availability in the understory.

To analyze the selectivity of the diet, we purposely excluded from the analysis grass-like species belonging to the Juncaceae and Cyperaceae families (grass-like). Apart from being their biomass insignificant in the understory as compared to that found in the adjacent vegas, where they dominate, our objective was to determine selectivity only for those species typical of that understory.

Data analyses

The assumption of normality (Shapiro-Wilks) was investigated for the variables species and groups of species percentage in the diet. Mean differences of dietary composition between seasons was performed by using the Student T test ($p < 0.05$) for paired samples, with $n = 3$.

Linear mixed-effect models were used to analyze the effects of treatments: Site: MC, R1 and R2, and Season: spring and summer, on the biomass available. Treatments (Site, Season and Site * Season interaction) were considered as a fixed effect, and the variable transect was considered as a block (random effect). The amount of the model variance that was explained by differences among sites was calculated by dividing the random effect variance by the total variance.

The mean differences of D index between seasons was performed by using the Student T test ($p < 0.05$) for paired samples, with $n = 3$.

This test was applied by using the Satterthwaite correction in the case the variances were not homogeneous ($p < 0.05$). All statistical analyses were performed by using the INFOSTAT Statistical Software (Di Rienzo *et al.*, 2015).

Results

Guanacos' diet composition

The percentages of the different groups of plants composing guanacos' diet during spring and summer, in the three study sites, is shown in Table 2. In the two seasons studied and considering all sites together, guanacos' diet presented high percentage of tree lenga beech leaves and twigs (38.7%), followed by grass-like (27.6%) and grass species (27.3%), and showing a low presence of herbs (3%), Lichens (2.1 %) and shrubs (1.2%). The most important items found in the diet, with frequencies higher than 10%, were *Nothofagus* sp. (mainly lenga beech leaves and shoots), *Uncinia lechleriana*, *Poa* sp, *Carex* sp. and *Festuca* spp. In spring, 55% of the diet was

Table 2. Percentage values (\pm S.E.) of plant species found in guanacos' diet during spring and summer, in the three sites (María Cristina (MC), Reserve 1 (R1), and Reserve 2 (R2), respectively). Student T test ($p < 0.05$) for paired samples, * denotes significant differences between seasons. The + denotes species characteristics of the vegas which presented low biomass in the forest.

Species	MC	R1	R2	Average	MC	R1	R2	Average	T
	Spring				Summer				
Tree leaves and shoots									
<i>Nothofagus</i> spp.	49.6	37.8	56.6	48.0 (5.5)	33.5	27.9	27.0	29.5 (2.0)	3.2*
Total	49.6	37.8	56.6	48.0 (5.5)	33.5	27.9	27.0	29.5 (2.0)	3.2*
Grass-like									
+ <i>Carex</i> spp.	16.8	17.7	13.3	15.9 (1.3)	25.6	13.5	22.5	20.5 (3.6)	1.2
+ <i>Uncinia lechleriana</i>	11.6	20.1	9.8	13.8 (5.5)	0	6.5	4	3.5 (1.9)	2.8*
+ <i>Luzula</i> spp.	0	0	0	0	0	3.2	1	1.4 (0.9)	1.5
Total	28.4	37.8	23.1	29.8 (4.3)	25.6	23.2	27.5	25.4 (1.3)	0.9
Grasses									
<i>Bromus coloratus</i>	1.3	1.2	0.7	1.1 (0.2)	1.9	1.6	1.5	1.7 (0.1)	2.7
<i>Festuca</i> spp.	1.9	1.2	0	1.1 (0.5)	11.2	2.7	2.5	5.4 (2.9)	1.5
<i>Poa</i> sp.	13.6	16.5	9.1	13.1 (2.1)	22.8	39.8	34.5	32.4 (5.0)	3.5*
Total	16.8	18.9	9.8	15.2 (2.7)	35.9	44.1	37.5	39.5 (2.4)	6.6*
Shrubs									
<i>Berberis</i> spp.	0	1.2	0.7	0.6 (0.3)	0	0	1	0.3 (0.3)	0.6
<i>Gaultheria</i> sp.	0	0.6	0	0.2 (0.2)	2.3	0	1.5	1.3 (0.7)	1.5
Total	0	1.8	0.7	0.8 (0.5)	2.3	0	2.6	1.6 (0.8)	0.8
Herbs									
<i>Osmorhiza chilensis</i>	3.9	0	7	3.6 (2.0)	1.4	3.8	2	3.1 (0.7)	0.6
Total	3.9	0	7	3.6 (2.0)	1.4	3.8	2	3.1 (0.7)	0.6
Lichens									
Total	1.3	3.7	2.8	2.6 (0.7)	1.4	1.1	2.5	1.7 (0.4)	1.1

composed of species only found in the forest understory (*Nothofagus* sp., *Osmorhiza chilensis*, *Berberis* sp., *Gaultheria* sp. and lichens), while 30% corresponded to grass-like species only found in vegas. The rest of the diet (15%) corresponded to other grass species found in either the forest understory or in the nearby vega. During the summer, the percentage of *Nothofagus* spp. in the diet significantly decreased in all three sites (29%, $p: 0.03$) and increased the grass component (40%, $p: 0.003$). The grass-like species showed a mean percentage of 25% in the diet in the two seasons analyzed. Of these grass-like species, *U. lechleriana* marginally decreased ($p: 0.05$) its frequency during the summer (Table 2).

Biomass availability in the understory

Total biomass showed significant differences among sites, being higher in R2 in both seasons analyzed and lower during spring in R1 and in summer in MC (Table 3). The higher values found in R2 could be related to the higher lenga seedling and sapling biomass availability as compared to the other sites. The lowest lenga seedling and

sapling biomass availability in R1 and MC were registered during the summer season (Table 3). Biomass of all other analyzed groups of species did not show significant differences. However, biomass of grasses presented a maximum value (~ 160 kg DM ha⁻¹) in R2 and a minimum (~ 50 kg DM ha⁻¹) in MC, both during the spring. All other herb species showed a peak of biomass (~ 115 Kg DM ha⁻¹) in R2 during the summer and a minimum (~ 18 kg DM ha⁻¹) in R1 also during the summer. Shrub biomass was in general scarce (< 1 kg DM ha⁻¹) in all three sites. In neither case, the seasons considered nor the interaction between season and site did show significant differences (Table 3).

Considering the relative availability of each group related to the total understory biomass, it was observed that the group of grasses predominated, followed by trees and herbs. Shrubs, showed a very limited availability (Figure 2).

Guanaco selectivity of forest understory species

The Ivlev's index showed that lenga regeneration (seedlings and saplings) were selected or consumed in

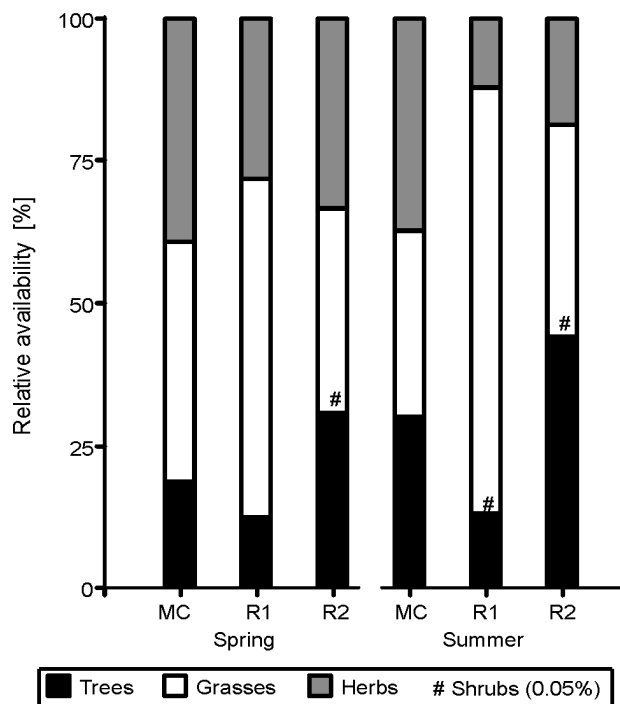


Figure 2. Relative availability of the different groups of species as related to total forage availability in the understory, in spring and summer and for the three studied sites in Tierra del Fuego, Patagonia, Argentina (María Cristina (MC), Reserve 1 (R1), and Reserve 2 (R2), respectively).

relation to its availability in all three sites and during both seasons (Figure 3). In spite of their low availability, shrubs were also highly selected. Herbs were rejected in all three sites during both seasons. Grasses, instead, were rejected during spring and consumed according to their availability, or slightly selected, during summer, being significant the consumption difference between seasons (spring and summer) ($T: 3.29$, $p: 0.03$, Figure 3).

Discussion

Guanacos' diet composition

In the particular environments that compose the landscapes of Tierra del Fuego, in which *Nothofagus* forests are intermixed with vegas, guanacos' populations may show either migratory or sedentary behavior (Raedeke, 1982; Schiavini *et al.*, 2009; Moraga *et al.*, 2015). Some studies showed that guanacos migrate to lowlands and coastal areas of Tierra del Fuego during cold winter periods, returning to forest areas of higher altitudes in spring and summer (Raedeke, 1980; Bonino & Fernández, 1994; Montes *et al.*, 2000), or mainly during the summer (Moraga *et al.*, 2015). Schiavini *et al.* (2009), however, found that there are sedentary guanacos populations that remain in the forests and surrounding vegas of Tierra del Fuego all year around. While guanacos in the three studied sites may have shown different migratory behavior, we restricted our study to determine their diet during the relatively warm period comprising from mid spring to mid-summer, when the populations wandered around *Nothofagus* forests and vegas. During these periods, high amounts of leaves and twigs of seedlings and saplings of *Nothofagus* spp., and also of grass species (mainly of *Poa* sp. and *Festuca* sp.), were consumed by guanacos; grass-like species such as *Carex* sp. and *U. lechleriana* completed its diet. The consumption pattern was similar in the three analyzed sites. These results are in accordance with some studies carried out in other areas of Tierra del Fuego (either in Chile or Argentina) (McNaughton, 1983; Bonino & Pelliza Sbriller, 1991; Muñoz González, 2008; Soler Esteban *et al.*, 2013),

Table 3. Average values of available understory biomass in kg DM ha⁻¹ (\pm S.E.) in spring and summer, and in each studied site (Estancia María Cristina (MC), Reserva Corazón de la Isla 1 (R1), Reserva Corazón de la Isla 2 (R2)). Different letters indicate significant differences ($p < 0.05$, LSD Fisher) between sites and season.

Season	Site	Total	Trees (leaves and shoots)	Grasses	Herbs	Shrubs
Spring	MC	176.5 (27.3) bc	47.4 (8.5)bc	51.2 (16.3)	58.2 (12.8)	0
	R1	124.4 (39.2) c	20.7 (6.9) c	85.5 (32.6)	18 (7.7)	0.06 (0.06)
	R2	478.6 (113.7) a	188.9 (53.9) a	159.9 (45.6)	98.4 (40.5)	0.3 (0.3)
Summer	MC	161.5 (33.5) c	28.7 (7.5) c	65.4 (25.4)	60.9 (14.2)	0
	R1	185.4 (46.3) bc	27.7 (9.6) c	110.1 (36.2)	52 (14.8)	0
	R2	347.3 (68.5) ab	106.5 (29.9)b	125.1 (30.3)	115.2 (36.8)	0.15 (0.15)
Site F (p)		10.6 (0.01)	13.6 (0.006)	3.5 (0.09)	2.18 (0.19)	0.82 (0.48)
Season F(p)		0.3 (0.58)	2.34 (0.13)	0.002 (0.96)	0.78 (0.38)	0.30 (0.58)
Site * Season		1.15 (0.32)	1.39 (0.25)	0.5 (0.61)	0.20 (0.82)	0.11 (0.89)
Random effect variance (transect)		6.9E-05	9.9E-05	5.4E-05	0.28	0.28

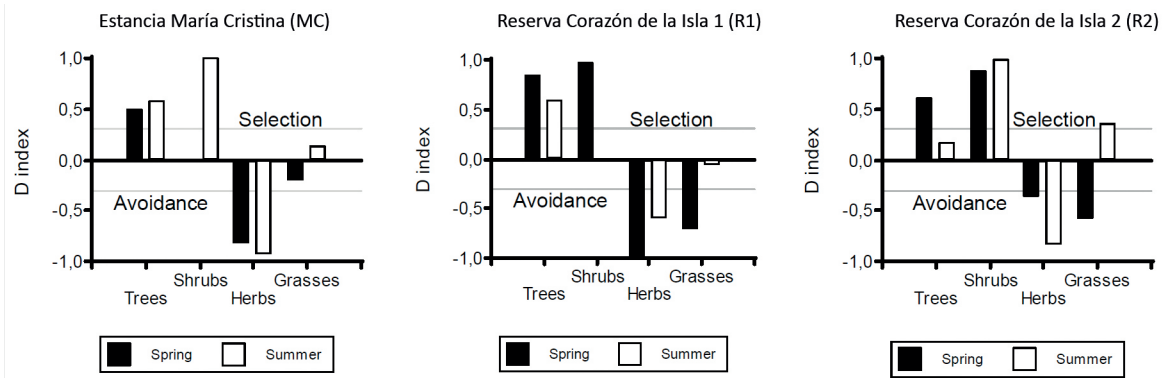


Figure 3. Selectivity index (Ivlev's index modified for Jacobs, 1974) of guanacos for the different plant groups available in lenga beech forest understory from three sites at Tierra del Fuego, Patagonia, Argentina: Trees (*Nothofagus* sp. leaves and twigs of seedlings and saplings), Shrubs, Herbs and Grasses. Values > 0.3 indicated selection and < -0.3 indicated avoidance.

and emphasize the importance that *Nothofagus* spp. leaves and twigs have in guanacos' diet during the spring in this island (Soler Esteban *et al.*, 2011). Our results, however, highly contrast with guanacos' diet determined in other environments outside Tierra del Fuego. In continental Patagonia, for instance, it has been demonstrated that guanaco diet overlap with that of sheep during the summer season, when both species feed on grasses and grass-like species found in meadows (Baldi *et al.*, 2004). During the winter months, instead, guanaco shifts its preference to shrubs (*Senecio* spp., *Mulinum* spp., *Berberis* spp.), which comprise about 55 to 80% of its diet during this cold period (Baldi *et al.*, 2006). In the north-central region of Argentina (in the provinces of Mendoza and Córdoba), several studies revealed that guanacos mainly consume grass species, shifting their preferences to some portions of woody species only when grasses are very scarce (Puig *et al.*, 1997; Barri *et al.*, 2014). It is interesting to note that this north-central region includes a variety of environments in which the trees *Polylepis australis* and *Maytenus boaria* are abundant. While leaves of these species are highly preferred by domestic grazers (cows, goats, and sheep) (Renison *et al.*, 2015), guanacos prefer to graze on short grasses, avoiding foraging on these and other tree species (Flores *et al.*, 2013).

Despite the abundant offer of herbaceous species during spring and summer in the areas surveyed in Tierra del Fuego, our results showed some preference of guanacos to browse on *Nothofagus* spp. leaves and twigs to satisfy part of their nutritional requirements. This particular feeding behavior may be related to the efficiency of gastric digestion that guanacos have (Marín *et al.*, 2006). In fact, guanacos and other camelids regurgitate and re-chew the forage they eat, and are much more efficient than ruminants in extracting protein and energy from poor quality forages (San Martín & Bryant, 1989; Pinto Jiménez *et al.*, 2010). On the other hand, the corporal mass plays an important role in the

foraging strategy (Gordon, 2003). In this regard, it has been proposed that an inverse relationship exists between body size and selectivity, being the guanaco a herbivore with an intermediate selectivity (species from 50 to 200 kg of body weight (Baldi *et al.*, 2004).

Guanaco selectivity of forest understory species

The analysis of diet selectivity of guanacos, taking into consideration exclusively species grown in the forest understory (excluding grass-like species), showed that they prefer to consume woody vegetation (leaves and twigs of lenga seedlings and saplings) and grasses only during the summer, avoiding selecting grasses during the spring, and herbs during either spring or summer. Other studies carried out in Tierra del Fuego emphasized the high frequency of lenga leaves and twigs found in the diet of guanaco, although neglected the importance of shrub species in that diet (Martínez Pastur *et al.*, 2010; Soler Esteban *et al.*, 2011; Arias *et al.*, 2015). In our study, however, although we recorded little abundance of shrubs in the forest understory and that these species were infrequent in the diet, the Ivlev's index indicated that shrubs are highly preferred should they are available.

On the other hand, although the availability of herbs was relatively high related to the total available biomass inside the forest (and much higher if we consider the adjacent vegas), they were rejected by the guanacos, coinciding with the results presented by other studies (Soler Esteban *et al.*, 2011; Muñoz & Simonetti, 2013). Grasses, instead, although rejected during spring, they were slightly selected during the summer and consumed according to their availability. Contrasting with our results, Puig *et al.* (2011) indicated that in steppe zones of Central Argentina, grasses and graminoids species were preferred by free ranging guanacos, and that woody species were rejected. Furthermore, these authors reported that in these steppe zones, wetland meadows

constitute a focal sector for guanacos foraging. Based on the classification proposed by Hofmann (1989) the guanaco could be then defined as an intermediate herbivore, or opportunistic (mixed) feeder. This is so because it forages on a highly diverse range of food sources (González *et al.*, 2006a), having developed physiological and morphological adaptations for including in its diet a high proportion of woody species (Searle & Shipley, 2008). In continental Patagonia, the negative impacts of understory grazing by domestic and wild ungulates has been considered as one of the most important disturbances that affect *Nothofagus* forests regeneration (Veblen *et al.*, 1992; Relva & Veblen, 1998; Raffaele *et al.*, 2011; Barrios-García *et al.*, 2012). In this region, guanacos avoid grazing on *Nothofagus* forests. In Tierra del Fuego, instead, guanacos select feeding areas within *Nothofagus* forest in spring and summer, despite these are seasons of great abundance of other forages outside the forest. The significant consumption of lenga could adversely affect the development of regeneration of the species, and this aspect should be carefully considered in planning and implementing management plans for sustainable regeneration and growth of *Nothofagus* forests. In order to cast light on this issue, it is necessary that future research should be focused in determining vegetation dynamics comparing grazed and ungrazed lenga forests in Tierra del Fuego.

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