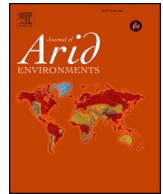




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Effect of population density on diet composition and dietary niche breadth of guanaco (*Lama guanicoe*, Müller 1776) in northeastern Patagonian steppes

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ABSTRACT

The optimal foraging theory postulates that as animal population density increases, the progressive decline in preferred forage availability results in changes in diet composition and widening of dietary niche breadth. For sedentary guanaco populations, some authors proposed a mechanism of population density limitation below the environmental carrying capacity, mediated through territoriality. Under the optimal foraging theory, increased density would lead to changes in guanaco diet selectivity and composition. Conversely, under the self-regulation hypothesis, guanacos would not affect preferred forage availability and no differences in guanaco diet would be expected. We tested these contrasting hypotheses by assessing both the differences in the proportion of grasses and shrubs present in guanaco diet and dietary niche breadth at three contrasting densities in northeastern Patagonian steppes. We did not find guanaco density effects on preferred forage availability, grass-shrub proportions in the diet and diet selectivity. Guanacos showed a mixed diet composed by plant species of both high and low nutritional quality independently of population density. The lack of changes in diet composition suggests that guanacos did not perceive a restriction in forage availability in terms of either biomass or nutritional content, regardless the observed increase in population density.

1. Introduction

The optimal foraging theory is a useful conceptual framework to test hypotheses on foraging behavior and diet selection. A postulate of optimal foraging theory is that as animal population density increases, the progressive decline in preferred forage availability results in changes in diet composition. While herbivores at low densities will select near-optimal resources (Pianka, 1988), they will include a wider variety of less preferred items in their diet as intraspecific competition increases and preferred plant species become depleted (Owen-Smith, 1994). Consequently, at higher population densities, dietary niche breadth is expected to be wider, so that proportions of plant species or functional groups could be different from those observed at lower densities. This density-dependent dynamics of plant-herbivore interactions in which high herbivore density reduces forage availability was reported for various bottom-up regulated ungulates (Kie et al., 1980; Rooney, 2009; Nicholson et al., 2006), with the magnitude of the changes observed in diet composition resting on the degree of selectivity characteristic of each species (Svanback and Bolnik, 2007). These changes in forage availability and diet may have nutritional and energetic consequences

for animals, such as the reduction of the time spent in other non-feeding activities, and may exacerbate the impact of herbivores on the environment through adverse grazing effects on certain plant species and/or feeding sites (Roguet et al., 1998; Mysterud, 2006).

Information on how changes in population size affect resource selection is scant for most large mammals (Nicholson et al., 2006) and few studies have accounted for behavioral aspects such as territoriality when addressing these relationships (Mosca-Torres and Puig, 2010). Marino et al. (2016) found that in a Patagonian sheep ranch converted into a wildlife reserve, a sedentary population of guanaco (*Lama guanicoe*, Müller 1776) exhibited drastic changes in density, increasing rapidly during the first years after sheep removal and then stabilizing around a seemingly equilibrium point. This initial increasing density would have resulted from recruitment coupled with immigration of animals from neighboring sheep ranches (Marino and Baldi, 2014, and the bulk of these individuals constituted family groups (Marino et al., 2014). During the observed population trajectory, the expected effects of herbivore-density on preferred forage availability (grass biomass and cover) remained undetected. The authors proposed a mechanism of density limitation below the environmental carrying capacity, mediated

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by resource defense through territoriality (self-regulation hypothesis) in which density-dependence operates through dispersal rates, as an explanation for the lack of density effects on forage resources. This mechanism relies on the fact that guanaco males actively assess forage availability and defend an area large enough to monopolize the forage required by their females (Franklin, 1983). Average size of family groups at this location was six adults plus the young of the year, with no changes in the number of adults per family during the observed period (Marino and Rodríguez, 2017). The size of the family group is regulated by forced dispersal of both male and female juveniles and the typical non-acceptance of new adult females into the group. Male juveniles join non-territorial male groups while females may join provisionally either to male groups or to new family groups (Franklin, 1974, 1983). Under the assumption of no territory compression as density increases, the stated regulating mechanism may prevent nutritional restriction in spite of population growth since, once a territory is established, the access to forage resources by the members of a family group will not be affected by an increasing number of neighbors.

According to the classical perspective of the optimal foraging theory, progressive depletion of preferred plants due to increased guanaco density will lead to changes in guanaco selectivity and diet composition. In contrast, under the self-regulation hypothesis, territorial guanacos will not significantly affect preferred forage availability and no differences in guanaco selectivity and diet composition will be expected at different population densities. In order to test for these contrasting hypotheses, we assessed the differences in the proportion of grasses and woody plants present in guanaco diet (diet composition) and dietary niche breadth (selectivity) among territorial guanacos at contrasting densities along a population trajectory of increasing density in northeastern Patagonian steppes.

2. Methods

2.1. Study area

This study was conducted at the Reserva de Vida Silvestre San Pablo de Valdés (henceforth San Pablo), located in the south-west portion of Península Valdés (42°36' S; 64°15' W), Chubut Province, Argentina. San Pablo is a 73 km² ranch formerly dedicated to sheep production, which was purchased in 2005 by a local Non-Governmental Organization and converted into the present status of private wildlife reserve; all the c. 3500 sheep were removed and a permanent warden was appointed (Arias et al., 2017). The climate of this region is semi-arid with maritime influence. Mean annual temperature and annual precipitation in San Pablo were estimated in 13.4 °C and 232 mm, respectively (Frumento, 2017).

San Pablo encloses an area of high geo-edaphic heterogeneity, which determines the presence of a complex mosaic of eight vegetation communities (hereafter VC) inside the reserve (Bertiller et al., 2017; Pazos et al., 2017). For this study, we selected five of them, which cover c. 80% of San Pablo area: VC1 (surface of 8.4 km²): Shrub-grass steppe, dominated by *Chuquiraga erinacea* D. Don ssp. *hystrix* (Don) C. Ezcurra; VC2 (surface of 7.4 km²): Shrub-grass steppe, dominated by *Chuquiraga avellanadae* Lorentz, *Nassella tenuis* (Phil.) Barkworth (formerly *Stipa tenuis*), and *Piptochaetium napostaense* (Speg.) Hack.; VC3 (surface of 14.9 km²): Shrub steppe, dominated by *C. avellanadae*; VC4 (surface of 12.2 km²): Dwarf-shrub steppe, dominated by *Hyalis argentea* D. Don ex Hook. & Arn. var. *latisquama* Cabrera; VC5 (surface of 7.5 km²): Grass steppe, dominated by *Sporobolus rigens* (Trin.) E. Desv., *Poa lanuginosa* Poir., and *N. tenuis*. A detailed description of the vegetation communities is provided elsewhere (Burgi et al., 2012; Pazos et al., 2017).

2.2. Guanaco density and study layout

After the reserve creation in 2005, guanaco density inside San Pablo was estimated on a yearly basis, exhibiting drastic changes. Density

increased rapidly during the first years until 2012, when it reached a seemingly equilibrium point (Marino et al., 2016). During the 2012–2018 period, average density was 29.1 guanacos/km² (SD among years = 4.3) (Marino, unpublished data). The initial increment in population density was observed at both global (the entire reserve) and local (vegetation community) level. This increase was relatively sharper in more productive vegetation communities but, in all cases, densities remained under the environmental carrying capacity estimated for each VC. The increase in density resulted mainly from the rise of the number of family groups establishing territories at each VC (Marino and Rodríguez, 2017). Since the reserve creation, guanaco is by far the predominant herbivore in San Pablo in terms of both population size and forage consumption (Marino and Rodríguez, 2017; D'Agostino et al., 2017).

We evaluated the effect of guanaco density on diet composition and dietary niche breadth for three years during a period of sustained density increase: 2010, 2011 and 2013. Guanaco doubled its density during these three years, being 13.7 (± 2.7), 16.2 (± 2.5) and 26.4 (± 6.1) guanacos/km² (± SD), respectively (Marino et al., 2016). We assessed diet through the analysis of food items present in feces collected in those years. We also evaluated the availability of forage items in relation to guanaco density using data from a vegetation monitoring system established on the five selected vegetation communities. For this analysis, we used data for all years from 2009 to 2013 in order to describe the complete trajectory of these variables. In 2010, 2011 annual precipitation was close to the average value for the region (232 mm), while during 2013 rainfall reached 338 mm (Frumento, 2017).

2.3. Vegetation and precipitation data

We used both field data and MODIS satellite imagery to characterize vegetation in San Pablo during the study period. In order to evaluate plant community composition and availability of forage items (shrubs and perennial grasses), we used data from a vegetation monitoring system that was established at the study area in 2009. This system consists of five fixed sampling sites (one monitoring site per VC) freely accessible to herbivores that are yearly sampled following the MARAS protocol (Spanish acronym for Environmental Monitoring of Arid and Semiarid Regions) (Oliva et al., 2006; Pazos et al., 2017). Plant species cover was assessed in two 50 m-long transects at each monitoring site using the point-intercept method (Muller-Dombois and Ellenberg, 1974), recording canopy interceptions with a pin at 20 cm intervals. Only perennial species were considered.

Likewise, to account for the potential influence of changes in green forage availability on diet composition we used the Enhanced Vegetation Index (EVI) derived from MODIS satellite images as a proxy of plant green biomass (Pettorelli et al., 2005). The MODIS product selected has temporal and spatial resolutions of 16-day intervals and 250 m, respectively. We considered EVI values dated immediately before the collection of feces samples, and considered the pixel corresponding to the exact location of each monitoring site.

In order to evaluate the effect of precipitation on forage item availability, we use the rainfall records of the field station “Andres Johnson” obtained by the staff of San Pablo with a pluviometer.

2.4. Feces collection and analysis

Guanacos defecate in communal dung piles that can be used for several years, reaching a size up to 3 m in diameter (Raedecke, 1979). In the case of territorial groups (families), their members defecate in communal piles located inside the boundaries of their territory (Franklin, 1983), so that we assumed that feces of a given dung pile corresponded to animals of the family groups that are established and forage in this area. We collected ten guanaco pellets from about ten active dung piles detected within an area of 100 m around the monitoring site of each VC at the end of the summer. Late summer at this

location usually implies relatively high water stress and the lowest forage availability of the annual cycle, therefore herbivore intraspecific competition would be highest. Only fresh pellets were collected. For each VC, we obtained one pooled sample from all sampled dung piles.

Feces were oven-dried at 60 °C for 72 h, ground to < 1 mm in a Wiley-type mill, depigmented with 70% ethanol, cleared with domestic bleach, stained with safranin and finally mounted on a microscope slide with glycerine-jelly (Williams, 1969; Latour and Pelliza Sbriller, 1981). We determined the botanical composition of the diets by micro-histological analysis of plant epidermal and non-epidermal fragments in feces (Sparks and Malechek, 1968; Sepúlveda et al., 2004). We identified these fragments at the level of genera or species when possible. Five microscope slides were prepared per sample and 20 microscope fields were examined on each slide using 100× magnification (Holeček and Vavra, 1981). We obtained frequencies of each identified item following Holeček and Gross (1982), grouping them into 4 types according to life forms: grasses (Poaceae), graminoids (Juncaceae, Juncaginaceae and Cyperaceae), shrubs and herbs. Micro-histological analysis of feces is not an exact technique due to differential digestibility of plant species, but compared to other methods of diet composition assessment, including analysis of rumen samples, micro-histological analysis of feces provides similar results (Mohammad et al., 1995). Moreover, the possibility to collect feces of a relatively high number of animal makes this technique accurate and practical for evaluating diet of wild animals (Borrelli and Pelliza Sbriller, 2014) and has been widely used for guanaco (Pelliza Sbriller et al., 1997; Puig et al., 1997).

To relate vegetation data with guanaco diet analysis, the plant species recorded in the vegetation surveys were grouped according to the corresponding genus in cases where micro-histological identification at species level was not possible. Thus, we assumed that one genus includes any of the species belonging to it previously reported for the study area by Pazos et al. (2017). Therefore, *Poa* spp. could potentially include *Poa ligularis* Nees ex Steud. and *P. lanuginosa*; *Chuquiraga* spp. refers to *C. avellanadae*, *C. erinacea* ssp. *hystrix* and *C. aurea* Skotts; and *Stipa* spp. includes *Nassella tenuis*, *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *P. humilis* (Cav.) Romasch., *N. longiglumis* Phil. Barkworth, *Jarava neaei* (Nees ex Steud.) Peñailillo, and *Amelichloa ambigua* (Speg.) Arriaga & Barkworth. All these grass species belonged to the *Stipa* genus and were reclassified during the last decade.

2.5. Data analysis

We considered as forage items only those genera/species whose frequencies of occurrence in the diet were greater than 5% (Baldi et al., 2004). In order to assess changes in the availability of forage items during the study period, we fitted generalized linear mixed models to plant-cover data obtained from the vegetation monitoring system on each perennial species/genera that may turn out to be a forage item on guanaco diet at the area. In order to fit reliable models, only items whose frequencies in the transects were high enough to result in cover higher than 15% were modelled, whereas certain items that showed a cover less than 2% were excluded from the analysis. We assumed a Binomial error structure (number of interceptions for one species/total interception points) and a logit link function (Crawley, 2007). The fixed terms included in the model were guanaco density and annual rainfall, whereas monitoring site and transect identity were included as nested random terms to account for the lack of independence of the observations recorded on the same transect at each monitoring site.

We tested the stated hypotheses of the effect of guanaco density on both diet composition at the plant functional group level and dietary niche breadth. For diet composition, we firstly grouped genera/species into grasses and shrubs. Due to previous studies of guanaco diet for the region (Baldi et al., 2004; Pazos et al., 2013) point to perennial grasses as main forage, we focused analysis on the variations in the proportion of grasses in diet.

To characterize guanaco diet at each guanaco density, we used the proportional similarity index (PS) as a simple measure of niche breadth in each VC. The conceptual basis for variations in niche breadth is resource selectivity by the species (Petraitis 1979); because in natural communities the resources are not equally abundant, those niche breadth measures that do not include resource availability in environment could mislead the interpretation of species resources utilization (Feisinger et al., 1981; Hurlbert, 1978; Petraitis, 1979). PS was based on species/genera proportion in diet and in vegetation communities, and it ranges from 1.0 for the broadest possible niche (population uses resources according to their availability) to 0.0 for the narrowest possible niche (population is selective and use exclusively the rarest resource) (Feisinger et al., 1981). Complementarily, we calculated the Ivlev (1961) index for each forage item in 2009, 2011 and 2013 to evaluate dietary preference. We established -0.3 and 0.3 as thresholds for the indifference rank (i.e. use proportional to availability); values between 0.3 and 1 indicated preference and values between -0.3 and -1 indicated avoidance (Puig et al., 1996).

We then fitted linear mixed models on the proportion of grasses in the diet and on niche breadth (PS). We compared model performance of different combinations of fixed effects, including guanaco density, annual rainfall and EVI. The identity of the VC was included as a random term to account for the potential inter-dependence of the feces collected in the same vegetation community. Model selection was based on Akaike's information criterion corrected for small samples (AICc), selecting a subset of models based on a delta AIC < 2 in relation to the model having the lowest AIC. Among these candidates, we considered the most parsimonious model as the best alternative (Crawley, 2007).

3. Results

3.1. Availability of forage items

The species/genera with frequencies higher than 5% in diet and, consequently, considered as forage items were five grasses: *Poa* spp., *P. napostaense*, *P. urvilleanum*, *Stipa* spp. and *S. rigens*; and six shrubs: *Chuquiraga* spp., *H. argentea*, *Brachyclados melaganthus*, *Ephedra ochreatea*, *Schinus johnstonii* and *Mulguraea ligustrina*. The shrubs *B. melaganthus*, *E. ochreatea*, *S. johnstonii* and *M. ligustrina*, showed cover values lower than 5% during the study period (data not shown) and therefore were excluded from the availability analysis.

The availability of forage items measured as plant cover varied during the study period (2009–2013) in different ways (Table 1a). Guanaco density and *S. rigens*, *Chuquiraga* spp. and *H. argentea* cover were not significantly related (Table 1a). *Poa* spp. cover decreased in 5.7% as guanaco density increased during the study period, while *P. napostaense* and *P. urvilleanum* cover increased with guanaco density in 4.7, and 11.2%, respectively (Table 1b). Except for *Stipa* spp., plant cover of forage items was not significantly related to annual rainfall (Table 1a) during the study period. *Stipa* spp. cover increased with annual rainfall; moreover, once the rainfall effect was accounted for, the statistical significance of the guanaco density effect became negligible (Slope = -0.011 , Std. Error = 0.007, DF = 30, p-value = 0.139). This change indicates that these explanatory variables might be correlated (parameters correlation = -0.66) and that the effect of population density is trivial as a driver of cover variability of this plant genus when annual rainfall is considered in the analysis.

3.2. Diet composition, niche breadth and selectivity

Guanacos consumed both grass and shrub species, which accounted for 95–98% of their diet. Grasses were more abundant than shrubs (mean frequency: 64 and 32%, respectively) in the diet at the three density scenarios, but *Chuquiraga* spp. appeared as the third dietary item in importance, showing a frequency of occurrence of 10–20%

Table 1

Relationship between plant cover, guanaco density and annual rainfall for forage items present in guanaco diet at the study area. Standard error (SE); degrees of freedom (DF); b- Mean values of forage items cover (%), guanaco density (animals/km²) and annual rainfall (mm) during the study period.

Guanaco density						Annual rainfall				
Forage items	Value	SE	DF	t-value	p-value	Value	SE	DF	t-value	p-value
<i>Poa</i> spp.	-0.016	0.008	31	-2.111	0.043	-0.002	0.001	31	-1.298	0.204
<i>S. rigens</i>	-0.014	0.017	7	-0.814	0.442	-0.003	0.003	7	-1.350	0.219
<i>P. urvilleanum</i>	0.074	0.020	7	3.667	0.008	0.007	0.004	7	1.670	0.139
<i>Stipa</i> spp.	0.022	0.009	31	2.393	0.023	0.007	0.001	31	8.456	0.000
<i>P. napostaense</i>	0.120	0.024	19	4.986	0.000	-0.008	0.005	19	-1.828	0.083
<i>Chuquiraga</i> spp.	-0.001	0.003	23	-0.223	0.826	0.000	0.000	23	-0.996	0.329
<i>H. argentea</i>	-0.013	0.015	5	-0.859	0.429	-0.003	0.001	5	-2.251	0.074

	2009	2010	2011	2012	2013
<i>Poa</i> spp.	29.4	29.1	28.1	24.2	23.8
<i>S. rigens</i>	37.1	36.8	35.9	32.1	31.8
<i>P. urvilleanum</i>	5.0	5.3	6.6	15.1	16.2
<i>Stipa</i> spp.	17.6	17.9	18.9	23.6	24.0
<i>P. napostaense</i>	0.7	0.8	1.1	4.8	5.4
<i>Chuquiraga</i> spp.	24.4	24.4	24.3	24.2	24.2
<i>H. argentea</i>	24.8	24.6	23.9	21	20.8
guanaco density	11.5	12.5	15.5	28.0	29.1
Annual rainfall	229.1	211.7	212.1	210.7	338.4

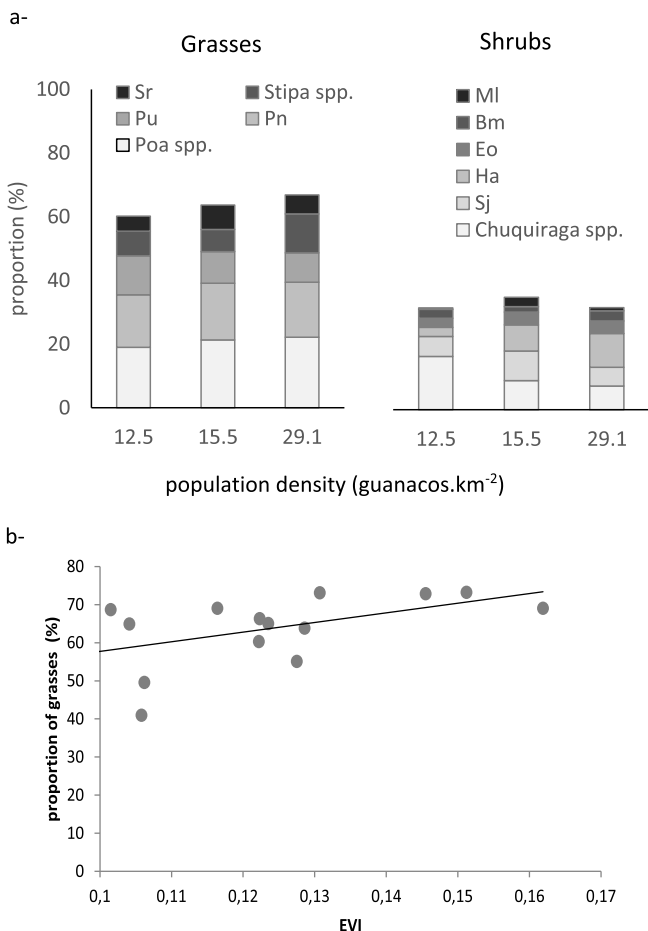


Fig. 1. a- Mean values of proportion of grasses and shrubs in guanaco diet at each population density. Pu: *Panicum urvilleanum*; Pn: *Piptochaetium napostaense*; Poa spp.: *Poa lanuginosa* and *Poa ligularis*; Sr: *S. rigens*; Stipa spp.: includes 5 reclassified species of the former genus *Stipa*; Bm: *Brachyclados melaganthus*; Chuquiraga spp.: *C. avellanadae*, *C. erinacea* ssp. *hystrix*, and *C. aurea*; Eo: *Ephedra ochreata*; Ha: *Hyalis argentea*; Sj: *Schinus johnstonii*; Ml: *Mulgoraea ligustrina*. b- Proportion of grasses in guanaco diet as a function of EVI for each VC registered for the three years of the feces collection (2010, 2011 and 2013).

Table 2

Model selection for proportion of perennial grasses present in guanaco feces and for the proportional similarity index (PS). Delta AICc refers to the difference between the score of the current model and that of the model with the lowest AICc. The final model selected for each of the response variables is the one with delta AICc of 0.

delta AICc						
Intercept	Guanaco density	EVI	Annual Rainfall	df	Proportion of Grasses	PS
+		+		4	0	0.59
+	+	+		5	4.87	11.08
+		+		5	6.28	12.66
+		+	+	5	9.96	17.08
+	+	+		6	12.19	24.38
+	+			4	14.09	11.43
+				3	14.61	0
+	+	+	+	6	14.8	27.95
+				4	14.86	12.57
+		+	+	6	17.18	30.66
+	+			5	19.53	25.02
+			+	4	21.52	16.22
+	+		+	5	22.13	27.43
+	+	+	+	7	23.49	42.49
+			+	5	24.94	29.77
+	+		+	6	28.65	42.15

(Fig. 1a). There were no significant effects of population density on diet composition in terms of the proportion of functional groups (Table 2). The only factor related to the observed variation in the proportion of grasses present in guanaco feces was the vegetation greenness proxy, EVI (Table 2), which resulted in an increase in the proportion of grasses consumed when the photosynthetic activity measured by this index was higher (Slope = 175.7; Std. Error = 50.9; DF = 9; t-value = 3.45; p-value = 0.007; Fig. 1b).

Regarding niche breadth, PS showed values ranging from 0.3 to 0.7 depending on the VC (Fig. 2) and it was not related to neither guanaco density nor to any other variable considered in the analysis (Table 2).

The Ivlev index indicated that *Stipa* spp., *Poa* spp., *S. rigens* and *Chuquiraga* spp. were the only genera/species consumed proportionately to their availability, whereas the rest of the species present in the samples were preferred by guanacos independently of population density (Fig. 3).

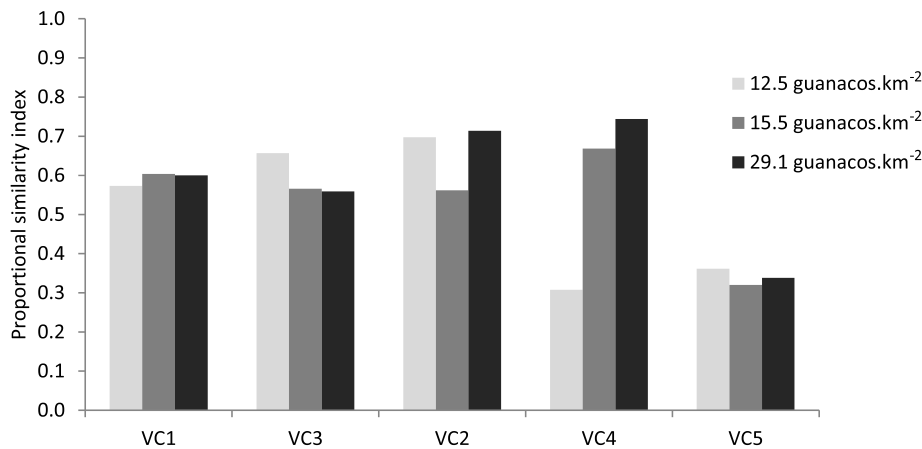


Fig. 2. Values of proportional similarity index calculated for each vegetation community (VC) and guanaco density.

4. Discussion

Between 2009 and 2013 guanaco density increased significantly within San Pablo Reserve. However, diet composition and niche breadth of guanacos did not vary despite this density increment. Based on the statements postulated by the optimal foraging theory, this result may be related to the lack of an appreciable reduction in the availability of main forage items. Accordingly to that framework, the lack of density effects would imply the absence of forage competition (Pianka, 1988) and also suggests a low/moderate grazing pressure on forage species (Mysterud, 2006). In our study, *Poa* spp. was the only species that showed a significant reduction in its cover with the guanaco density increment. Conversely, *P. urvilleanum* and *P. napostaense* increased their availability despite being highly preferred grasses. The slight but significant reduction in *Poa* spp. cover (5.6%) and the increments of the other species were not reflected in diet changes, suggesting that these variations were not enough to force animals to change their selectivity. Similar results were found by Folks et al. (2014) for white-tailed deer in a semiarid shrubland where drought but not population density influenced forage dynamics and dietary composition. Changes in vegetation predicted by optimal foraging theory due to increased herbivorous density may be less likely for arid environments due to weak coupling between grazers and vegetation (Augustine and McNaughton, 1998). Accordingly, emergence of density-dependent effects could be

infrequent in these environments where fluctuation in precipitation can have a greater influence on vegetation dynamics than herbivores (Ellis and Swift, 1988; Folks et al., 2014). In this sense, for our study area, variability in total perennial grass cover was independent from changes in population density but was coupled with precipitation (Marino et al., 2016; Marino and Rodríguez, 2017). However, and even though guanaco population appears to be stabilized around an equilibrium density since 2012 (Marino and Rodríguez, 2017; Marino unpublished data), vegetation changes found in this study deserve attention and stress the importance of assessing eventual long-term effects on guanaco diet. Particularly, in the case of *Poa* spp. the bulk of frequencies included in this genus recorded during the cover assessment correspond to *Poa lanuginosa*, a rhizomatous species with high nutritional quality and high short-term variability associated to rainfall events (Giraudó et al., 2012). Besides, *Stipa* spp. seems to be related to annual rainfall. This genus includes the species *Nassella tenuis* (formerly *Stipa tenuis*), which is the second grass species in terms of frequency at the study area and an important forage item. Therefore, further studies addressing grazer exclusion and precipitation variability effects are required to elucidate specific patterns.

In our study case, territorial defense is the mechanism shaping population density of guanacos and stabilizing it below the environmental carrying capacity assessed in terms of an equal share of available biomass of preferred grasses (Marino et al., 2016). However, the absence of

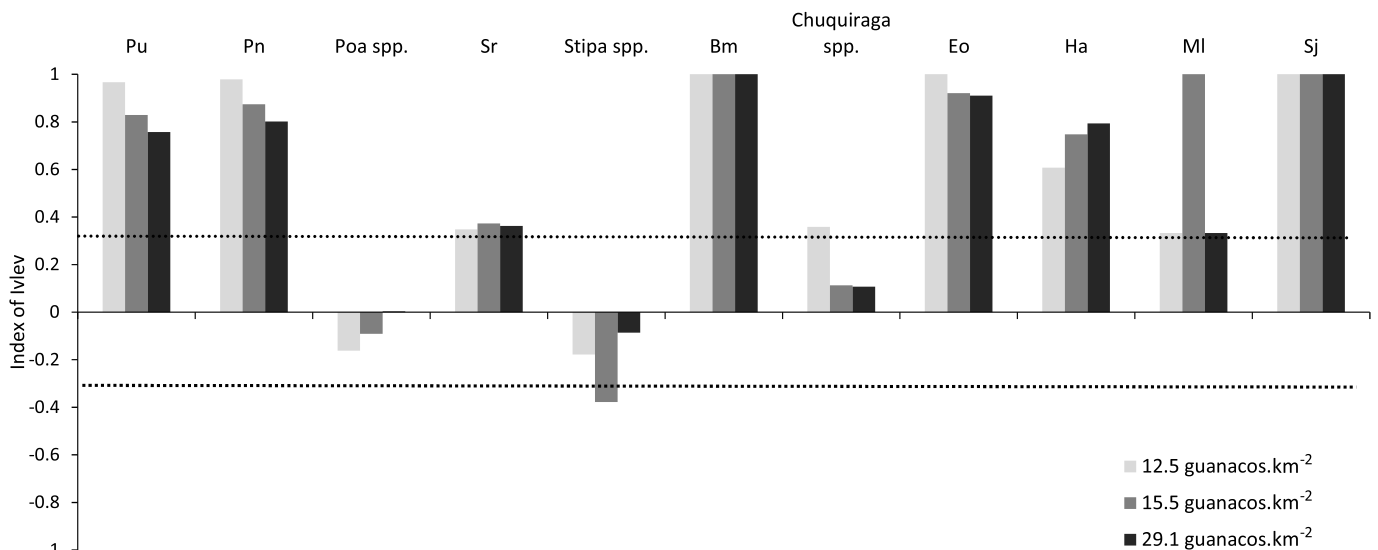


Fig. 3. Mean values of index of Ivlev at different population densities of guanacos. Dotted lines indicated the limits for the indifference rank (between -0.3 and 0.3). Acronyms for forage items as in Fig. 1.

limitation in the availability of forage biomass does not necessarily imply absence of nutritional restriction, and environmental carrying capacity may be lower than that assessed exclusively through forage biomass availability (Hobbs and Swift, 1985). In this sense, our results suggest no nutritional limitation since similar diet composition and dietary niche breadth were observed at contrasting population densities. This finding is consistent with the lack of population density effects on juvenile recruitment in the territorial groups at the study area and offers additional support to the hypothesis of self-regulation below environmental carrying capacity postulated by Marino et al. (2016).

At the three evaluated densities, the bulk of consumed items were grass and shrub species. Other plant forms as herbs, graminoids and cacti were consumed but they accounted for less than 5% of the diet (data not shown). Grasses were dominant in all cases but shrubs represented more than one third of the consumed items. A similar proportion of grasses and shrubs was observed in guanaco diets for other sites (Puig et al., 1996; Pelliza Sbriller et al., 1997), especially in summer months (Baldi et al., 2004). The values of the PS index indicated that guanacos showed intermediate selectivity, although selectivity appear to be higher at the grass steppe. In this sense, the same herbivore can show either a selective or an opportunistic foraging behavior depending on forage availability (Jaksic, 1989). *Stipa* spp., *Poa* spp., *S. rigens* and *Chuquiraga* spp. were the most abundant items at San Pablo and guanacos consumed them proportionally to their availability. Except for *Poa* spp., the nutritional quality of these species is relatively low in relation to the other consumed species (Somlo et al., 1985, 1997). Thus, their frequency in the diet could respond to a tradeoff between the more abundant though poor forage that would provide the required biomass, and less available species with higher nutrient content (Roguet et al., 1998). *Poa* spp., that showed the highest frequency in guanaco diet, has a relatively high protein content and digestibility in green tissues (Somlo et al., 1985), which points to *Poa* spp. as a key genus for guanacos in our study area. In this regard, dietary mixing may be a useful foraging strategy for ruminants to meet nutritional requirements (Hobbs and Swift, 1985), especially for territorial guanacos within a limited foraging area. The fact that South American camelids are physiological and anatomically adapted to the fibrous and low-quality vegetation dominant in arid environments (San Martín and Bryant, 1989) is consistent with this idea.

Guanacos were mainly described as grazers that can shift to browsing when grasses are not available or have low quality (Raedeke, 1979; Ortega and Franklin, 1988; Puig et al., 1996). Our results suggest that guanacos include a proportion of shrubs in their diet regardless of low availability of woody plants, such as in the grass steppe. Also, we found preferred species in both plant functional groups. In the Patagonian steppe, shrubs have higher protein content than grasses while grasses show higher digestibility and energy (Somlo et al., 1997). Mixed diets may optimize nutritional content and could avoid malaise due to ingestion of plants with high concentration of secondary compounds (Provenza et al., 2003). Additionally, at the end of the summer most grasses become senescent, lowering their nutritional value, while shrubs maintain green tissues and better nutritional quality (Somlo et al., 1987; Campanella and Bertiller, 2008). The advantage of including shrubs in the diet during the dry season has been highlighted for other herbivores inhabiting arid ecosystems, especially for lactating and pregnant grazers (Lambert et al., 1989). In the present study the proportion of grasses in the diet increased with EVI, suggesting that guanacos consumed more grasses when the later have more green biomass and therefore better quality. In this regard, rhizomatous grasses in our study area as *Poa lanuginosa* and *Panicum urvilleanum* can respond quickly to precipitation events making available new green biomass for herbivores (Girauco et al., 2012).

To conclude, the lack of changes in diet composition suggests that guanacos did not perceive a restriction in forage availability in terms of biomass neither nutritional content, regardless the observed increase in population density, supporting the idea postulated by Marino et al.

(2016) regarding the self-regulation mechanism for sedentary guanacos. In addition to the consequent limitation of herbivore density due to the mentioned mechanism, the ability of guanacos to select and consume a variety of plants yet in reduced geographical space (territories) implies a better distribution of grazing pressure on individual plants or species and resource exploitation. This ability was also pointed out as an ecological attribute that enables large herbivores to avoid over-utilization of forage resources, preventing environmental damage (Hart, 1985; Gordon and Lindsay, 1990), and highlights the importance of guanaco co-evolution with the Patagonian environment.

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