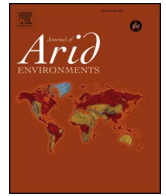




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On resource defense and sustainable grazing: Forage use by territorial and non-territorial guanaco groups

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ABSTRACT

Recent studies suggest that territorial defense can act as a regulating agent of herbivore density, buffering crowding effects and preventing vegetation depletion. The occurrence of territorial families and non-territorial male groups, both major social units in the social organization of guanacos, offers the unusual opportunity to test predictions about the role of territorial defense in buffering grazing impact. Under the hypothesis that forage use by guanacos in family groups would be less intense than that of male groups which lack territorial defense, we predicted that plant cover will be higher in areas used exclusively by family groups compared to that in areas used by male groups. The vegetation and the guanaco population at San Pablo reserve were being monitored for eight years showing that grass foliar and basal cover were reduced when non-territorial groups started using the monitored area, which was previously used exclusively by family groups. On a broader scale comparison, grass and basal cover were higher in areas used by territorial animals than in those used by non-territorial ones. The approximate area used intensively by the non-territorial groups represents less than 18% of the surveyed area, whereas most of the reserve is exposed to less intense use by the territorial family groups. Thus, temporal and spatial comparisons support the idea that the resource-defense system lowers the disturbance rate over vegetation resources by guanaco populations when compared with other ungulates lacking territorial behavior.

The study of grazing impact by large herbivores has been of main interest to ecologists and managers. The trophic cascades reported in the Northern hemisphere after predator removal have stressed the need to understand the regulation processes that shape plant-large herbivore dynamics in order to plan conservation initiatives and management decisions. On this regard, the role of territorial defense as a self-regulating agent of herbivore density has only recently been addressed (Marino et al., 2016). It has been suggested that territorial defense lowers the maximum disturbance rate over vegetation resources (Gordon and Lindsay, 1990; Nevo, 1979; Seabloom and Reichman, 2001; Seabloom and Richards, 2003), preventing overgrazing. However, this hypothesis has not been directly tested among large herbivores.

Guanacos and vicuñas are among the few species of large herbivores in which the interaction between territorial behavior and resource availability determines the spatial distribution of the individuals across the landscape (Franklin, 1983; Raedeke, 1979). Their mating system is known as resource-defense polygyny (Franklin, 1983). The main social units in this system are the family groups, composed of an adult male that defends a territory where a group of females with their offspring of

the year forage; male groups, that can reach hundreds of individuals and are composed mainly of juveniles and adult males; and solo males. Recent studies suggest that territorial defense by guanaco males in family groups acts as a regulating agent of population density, keeping the herbivore load proportional to the forage availability but under the environmental carrying capacity (Marino and Rodríguez, 2017; Marino et al., 2016). Thus, the guanaco mating system may buffer crowding effects and prevent vegetation depletion by promoting a relatively low-intensity, homogeneous resource use by the territorial groups.

The occurrence of both territorial families and non-territorial groups in guanaco populations offers the unusual opportunity to test predictions about the role of territorial defense in resource-use patterns. Such system predicts a low frequency of large aggregations of non-territorial animals and a high frequency of relatively small territorial families that are able to adjust their territory size to forage availability (Marino and Baldi, 2014). Resource-use patterns are expected to differ under similar conditions of herbivore density at landscape scale when aggregation patterns differ, because increased aggregation may promote increased heterogeneity in grazing intensity, entailing the concentrated use of certain patches. For example, a larger group implies a

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higher herbivore density at patch level and it is expected to exert a higher grazing intensity than various small groups using different patches would. Under the hypothesis that grazing intensity by guanacos in family groups would be lower than that of large male aggregations which lack the load-adjustment mechanism of territorial defense, we predicted that grass cover will be higher in areas used exclusively by family groups than in areas used by male groups. We conducted temporal and spatial comparisons to test this idea.

1. Guanaco and vegetation surveys

This study was conducted at San Pablo de Valdés (San Pablo), which is located on the Península Valdés (42°36 S; 64°15 W), Chubut Province, Argentina. In 2005, this 73 km² ranch formerly dedicated to sheep production was converted into a private wildlife reserve. San Pablo is delimited by 1-m-high wire fences, which restrict livestock movements from neighboring ranches. The guanaco population has been monitored since 2006 and vegetation performance has been assessed since 2009 by means of a permanent monitoring station set within each vegetation community (Marino et al., 2016). The guanaco population showed a noticeably recovery after the reserve implementation and since 2012 guanaco density fluctuates around 30 guanacos/km² (Marino et al., 2016). This communication is focused on data on a particular vegetation community present in San Pablo, where non-territorial groups were systematically observed during part of the study period. This community encompasses approximately 7 km² of grass steppe, dominated by *Sporobolus rigens*, *Poa lanuginosa* and *Nasella tenuis*, all perennial grasses. For a detailed description of the vegetation community see Burgi et al. (2012). Group sizes at the study site averaged 6 adults in families and ranged from three to 75 individuals in the highly variable male groups (Marino and Baldi, 2014).

The guanaco population at San Pablo has been surveyed 1–3 times each year since 2006. Post-reproductive surveys were conducted every summer with the exception of 2007. Data on winter-spring surveys were carried out during the 6 years of the study period and indicated that guanaco numbers were consistent with those obtained by post-reproductive surveys; we, thus, consider these summer estimates as our sample of population densities. Data collection on guanaco population was based on ground line transect surveys conducted along available dirt roads. A detailed description of guanaco surveys can be found elsewhere (Marino and Baldi, 2014; Marino et al., 2016). Population density was estimated by Distance Sampling (Buckland et al., 1993) that has proven to be a useful method to assess guanaco abundance in eastern Chubut (Baldi et al., 2001). Here we consider only local estimates for the specific vegetation community mentioned above. Density estimations were performed using Distance 5.0 software (<http://www.ruwpa.st-and.ac.uk/distance/>). According to the observed proportion of guanacos in families (territorial) and male groups (non-territorial), and the corresponding estimate of population density, we computed densities of guanacos in family groups and male groups for each year of the study period. These data allowed us to identify 2013 as the year when male groups were observed in the study area for the first time. Thus, we divided the study into two time periods, “pre male-groups” (2009–2012) and “male-groups” (2013–2016). In the “male-groups” time period, large male-groups (20–60 individuals) were systematically observed foraging around the permanent station used to monitor this vegetation community.

Temporal comparison: In order to assess temporal changes on the grass foliar (grass cover) and basal cover attributable to differential use by territorial and non-territorial groups, we modeled the data obtained at the only permanent monitoring station within this community. We recorded a number of variables on an annual basis (including perennial-grass cover and plant-basal cover) on two linear 50 m transect, using the point interception method at 20 cm intervals (250 points per transect) (Pazos et al., 2017). The spatial extent of this station is approximately 800 m² and it can be considered a representative patch of

this plant community in terms of floristic composition (Pazos et al., 2017). Perennial grasses were the only functional group present in the study area. This is the key functional group in guanaco diet across San Pablo (Pazos et al., 2013), thus cover of perennial-grasses can be considered as a proxy of habitat quality. Unlike grass cover, plant-basal cover is expected to be less sensitive to rainfall variability and to better reflect long-term changes driven by other factors (Herrick et al., 2005). We fitted a Mixed Effects Model (Crawley, 2007) to the data on grass foliar cover and grass basal cover, with the covariables “guanaco density” and “annual rainfall” and the factor “time period” as fixed effects. Transect ID was considered as a random term to account for the lack of independence within transects. Model selection was based on the AIC criterion, selecting a sub-set of models based on a delta AIC < 2 respect from the model having the lowest AIC. Among these candidates, we considered the most parsimonious model the simplest alternative (Crawley, 2007). Model fitting was performed using R software (version 3.2.5; the R Foundation for Statistical Computing, www.r-project.org).

Spatial comparison: In order to compare grass cover within sites intensively used by male groups and sites used mostly by family groups, we firstly defined an area with relatively high use by male groups. We computed kernel density estimations derived from all male-group locations recorded during the 2014–2016 population surveys, using SAGA GIS software (version 4.0.1, System for Automated Geoscientific Analyses, www.saga-gis.org). Group size was used to weight each location and each observation was assumed to have a decreasing influence up to 1 km radius, resulting in two equidistant contours. The area delimited by the higher density contour was considered as the core area used intensively by male groups. The surrounding area was considered as the alternative treatment, which consisted in a zone where the frequent family groups and some occasional male groups could be observed. According to our hypothesis, this area was expected to show higher cover values compared to the core area. In March 2016, we conducted 5 vegetation censuses inside the core area used by male groups and 5 outside this area and including locations where the observed guanacos were mostly in family groups. Different guanaco groups were observed grazing at each location therefore we considered that they were set far apart from each other so as to assume that spatial autocorrelation is negligible (Fig. 1). Each vegetation census consisted of two linear 50 m transects, along which we estimated perennial-grass cover and basal-plant cover using the point interception line method at 1 m intervals (Herrick et al., 2005). To compare grass cover between both areas we fitted a linear mixed model, including the treatment “territorial vs non territorial” as a fixed term and “site” as a random term in order to account for the interdependence of transects located in the same site. The same model was used to compare basal-plant cover between areas used by male groups and areas used by family groups.

2. Results and discussion

Kernel density estimations indicated that, during the 2014–2016 period, guanaco male groups used a core area of 1.3 km² and that this area included the location of the permanent station of the vegetation monitoring system used to assess plant community dynamics. According to the monitoring data, the variable that better explained the variation in grass foliar cover across 2009–2016 was “annual rainfall” and “time period” (Table 1). Grass cover increased with increasing rainfall (Slope = 0.41 SE = 0.09 t value = 4.78 Pr(> |t|) = 0.0005) and decreased by 52% on average after non-territorial groups started using the monitored area (Difference = -51.9 SE = 9.99 t value = -5.19 Pr(> |t|) = 0.0002) (Fig. 2). In contrast, basal plant cover showed no noticeable effects of annual rainfall (Table 1) but decreased by 6% on average after non-territorial groups started using the monitored area (Difference = -6.15 SE = 1.77 t value = -3.47 Pr (> |t|) = 0.0042). Regarding the spatial comparison, grass cover was on average 55.8% higher in areas exclusively used by family groups compared to areas used by male groups during the last three years



Fig. 1. Study area and the limits of the vegetation community. The area used intensively by male groups between 2014 and 2016 (dotted line); 2016 vegetation census locations: within the area used by territorial groups –family groups- (solid triangles); census locations within the area used intensively by non-territorial groups (plus signs); vegetation monitoring permanent station (square); male-group locations (empty circles); family groups locations (grey points); dirt road (double line).

Table 1
Model selection for grass foliar cover and basal plant cover.

Grass foliar cover models	Intercept	Density	Rainfall	Period	df	AICc	delta
7	49.67		0.413	+	5	148.6	0.00
4	100.5	-1.095	0.248		5	153	4.46
8	53.81	-0.100	0.402	+	6	153.9	5.29
2	156.5	-0.937			4	156.6	8.00
5	138.9			+	4	160.4	11.85
6	160.1	-1.274		+	5	160.5	11.91
1	125.7				3	160.6	12.07
3	82.92		0.173		4	162.2	13.6

Basal plant cover models	Intercept	Density	Rainfall	Period	df	AICc	delta
5	18.4			+	4	97.7	0
2	20.56	-0.159			4	98.3	0.62
6	19.61	-0.072		+	5	101.4	3.68
7	15.4		0.0139	+	5	101.4	3.72
4	22.36	-0.154	-0.008		5	102.4	4.71
1	15.32				3	103.2	5.53
3	19.89		-0.0185		4	106	8.33
8	17.37	-0.047	0.0084	+	6	106.5	8.85

(SE = 5.47; t value = 10.2; Pr(> |t|) = 0.000) (Fig. 3a). The coefficient of variation of grass cover was 9.6 and 19.7% respectively. The basal-plant cover was 4% higher in areas used by family groups (SE = 1.51; t value = 2.65; Pr(> |t|) = 0.029), where the coefficient of variation was 51.5%, in contrast to a 90.4% in areas used by male groups (Fig. 3b).

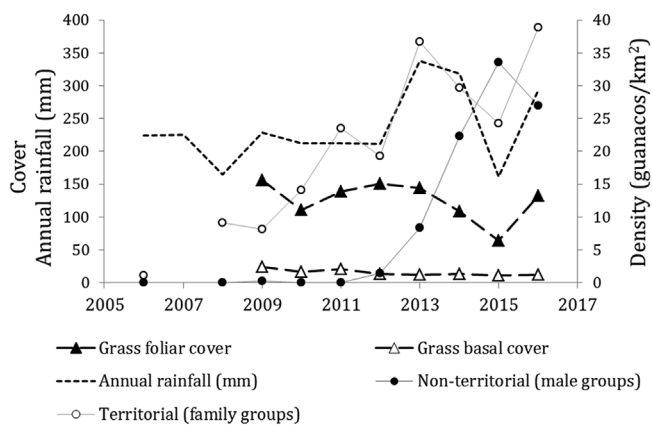


Fig. 2. Grass foliar and basal cover during the study period; annual rainfall; guanaco densities reported as individuals in territorial and individuals in non-territorial groups. Lines are for illustrative purposes only.

We hypothesized that grazing patterns under resource defense systems will result in a relatively low and homogeneous grazing pressure, with occasional patches of higher grazing intensity exerted by the scarce non-territorial groups. Temporal and spatial comparisons showed that, after accounting for rainfall effects, grass and basal-plant cover were lower and more heterogeneous in areas used by non-territorial groups than in areas used by family groups. Previous studies have assessed differences in habitat quality between areas used by guanaco families and male groups and suggested that this pattern was due to male groups being restricted to marginal habitats by the territorial males that monopolized the best areas (Franklin, 1983; Raedeke, 1979). In the present study, the time-series analysis indicated that grass and basal-plant cover were higher before non-territorial groups started using the area, suggesting that the particular use by these social units rather than a primary difference in habitat quality was the factor responsible for the between-areas differences. These results are consistent with the hypothesis that grazing pressure in areas used by territorial guanacos is lower than that of non-territorial ones. Mosca Torres and Puig, 2010 found that in a vicuña (*Vicugna vicugna*) population from Northern Argentina, the area used by a family group showed a lower and sharper seasonal decline in vegetation cover than the area used by male groups. However, group sizes and density asymmetries between family and male groups, and other relevant differences between studies preclude a deeper comparison among them.

Regarding the spatial extent of the observed patterns, it is worth mentioning that the area used intensively by non-territorial groups according to our kernel approach represented the 18% of the area surveyed in the particular vegetation community considered here and less than 5% of the entire vegetation area surveyed in the reserve. Moreover, male-groups are mobile and wander among vegetation communities within and between years. At the San Pablo reserve, male-groups have been observed almost exclusively in vegetation communities dominated by rhizomatous grasses, which can be considered to have a relatively high resilience (Pazos et al., 2017). The fact that grass cover increased in the last year of the study after the density of guanacos in male-groups declined is consistent with this observation. Therefore, the guanacos in the study area seemed to exert a widespread and relative moderate grazing intensity, with occasional patches exposed to ephemeral and relatively high grazing pressure by the scarce non-territorial groups.

It has been suggested that guanaco territorial defense acts as a self-regulating mechanism that allows to actively adjust herbivore density to forage availability and thus to buffer the typical productivity fluctuations of arid and semi-arid environments, such as those frequently observed across the Patagonian steppe (Marino et al., 2016). Augustine (2010) reported a similar dynamic for the territorial dik dik (*Madoqua*

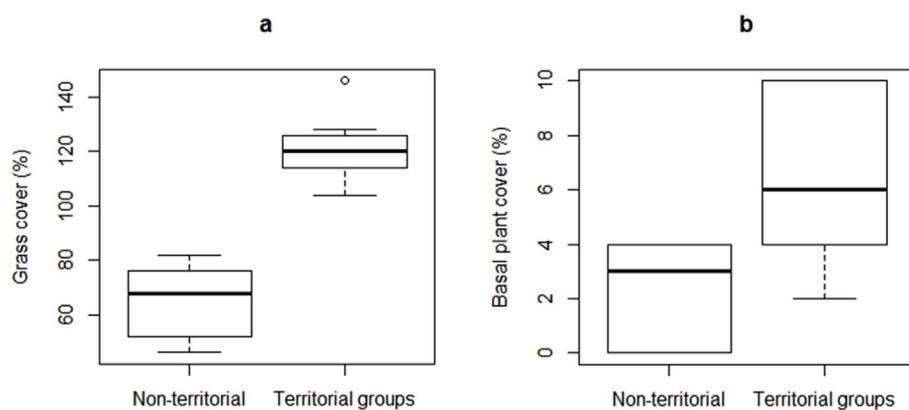


Fig. 3. Grass foliar cover (a) and basal cover (b) assessed in areas used by non-territorial groups and territorial groups in March 2016. The vertical dashed lines show one of two things: either the maximum value or 1.5 times the interquartile range of the data, whichever is the smaller. Points more than 1.5 times the interquartile range above the third quartile and points more than 1.5 times the interquartile range below the first quartile are defined as outliers and plotted individually.

kirkii) in Kenya. One of the key predictions derived from such systems is a lower disturbance rate over vegetation resources when compared to herbivores lacking territorial behavior (Seabloom and Richards, 2003). Although this is an un-replicated natural experiment and further research is required to assess the scope of these results, this study represents an additional piece of evidence suggesting that guanacos exert a lower intensity, more homogeneous grazing than other herbivore species that lack this regulation system.

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