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## Original Article

# Resource-defense polygyny and self-limitation of population density in free-ranging guanacos

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Although ecologists and managers have been increasingly preoccupied with the crowding consequences of overabundant herbivores, the potential role of territorial behavior as a self-regulatory agent has seldom been considered. The crowding mechanism underlies most regulation models in ungulate demography and relies on the assumption of an equal share of available supplies among individuals. In contrast, in territorial systems dominant individuals monopolize resources, predicting deviations from the expected demographic outcomes under the crowding approach. We used empirical data on a protected guanaco (*Lama guanicoe*) population to test competing hypotheses about crowding and territorial defense as the mechanism driving density regulation in a resource-defense polygyny ungulate. We assessed density dependence on recruitment at different spatial scales and density effects on preferred forage availability. The guanaco density inside the reserve increased rapidly and then stabilized during the last third of the study period. The absence of density effects on recruitment questions the existence of crowding mechanisms. Guanaco numbers stabilized below the environmental carrying capacity predicted by an equal share of available forage, supporting territorial defense as the mechanism shaping population density in the area. Variability in forage cover was independent from changes in population density, rejecting crowding effects on food supplies. These results are consistent with the hypothesis of a self-regulatory mechanism derived from resource defense that may prevent overgrazing. Our findings suggest that other factors in addition to food availability may determine the demographic carrying capacity under resource defense systems, stressing the importance of accounting for behavioral traits when addressing management issues.

**Key words:** carrying capacity, density regulation, *Lama guanicoe*, recruitment, territorial defense.

## INTRODUCTION

Large herbivore densities in lightly hunted, predator-free populations can grow excessively, leading to adverse effects on biodiversity and economic activities (Festa-Bianchet 2007). For example, some herbivore populations may not stabilize at levels where vegetation regeneration is possible, affecting succession, vegetation structure and composition, nutrient cycling, and other animal groups through habitat alteration (Gordon et al. 2004; Festa-Bianchet 2007). Trophic cascades triggered by cervid overabundance after predators' removal in the northern hemisphere are well-documented examples that have stressed the debate on the relative importance of top-down (i.e., mediated by top predators) versus bottom-up (i.e., mediated by food supply) regulation (Gordon et al. 2004; Festa-Bianchet 2007). In some of these disturbed scenarios

herbivore–vegetation equilibrium does not appear possible without human intervention (Festa-Bianchet 2007). Consequently, ecologists and wildlife managers are increasingly preoccupied with the negative impacts of high ungulate densities on biodiversity. In this context, understanding the mechanisms underlying density regulation and resource-use patterns by large herbivores becomes critical in order to predict potential foraging impact and design successful management plans (Rodenhouse et al. 1997; Gordon et al. 2004).

Population regulation necessarily implies a negative feedback between population growth and population density. The most cited regulatory mechanism has been focused on crowding effects and referred to as unadapted or scramble competition (Berryman 1999) or interference competition (Rodenhouse et al. 1997, 2006). Here, interference does not refer to the direct physical exclusion of competitors but to density-dependent, incidental, and unorganized exploitation competition over scarce resources (Rodenhouse et al. 1997; Berryman 1999; Rodenhouse et al. 2006). The crowding hypothesis is inspired by the ideal free distribution in which each

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individual is free to move from one patch to another, has the same competitive ability, and shares an equal portion of resources to the rest of the individuals in the population. Under this mechanism, the increase in population density reduces the per capita resource supply and realized suitability for all the individuals present in a given habitat, and eventually reproductive output and/or survival, decrease by crowding effects (Fretwell and Lucas 1969; Rodenhouse et al. 1997). As a result, population growth decelerates until carrying capacity, often referred as to  $K$  by population ecologists (Begon et al. 2006), is reached. However, in grazing management usage, carrying capacity is defined by the environment's response to differential grazing intensity (i.e., a threshold of adverse effects on resource supplies) (Valentine 2000), and this concept is usually extended to the management of wild herbivores in productive lands. Herein, we will use the terms demographic carrying capacity ( $K$ ), defined by a null instantaneous rate of increase in population density (i.e., the population density at equilibrium) within a fixed area, and environmental carrying capacity (CC), defined as the maximum population density that a particular environment can support without undergoing detrimental effects. Therefore, demographic carrying capacity must be computed with regards to population performance, whereas environmental carrying capacity must be computed with regards to forage availability and both terms do not necessarily refer to the same population density. Hence, when population density exceeds environmental carrying capacity, negative consequences due to resource overexploitation are expected.

Although the crowding approach has been successfully applied to account for intraspecific competition in population models, the ideal free distribution hardly applies if some individuals monopolize resources preventing others from using them. This is the case of a territorial species, in which subdominant individuals are forced to use poorer habitats or delay breeding (Fretwell and Lucas 1969; Rodenhouse et al. 1997; López-Sepulcre and Kokko 2005). Several mechanisms by which territorial species might be regulated have been proposed as alternatives to the crowding approach (Rodenhouse et al. 1997). According to these mechanisms, population density would increase until all available territories within a fixed area become occupied (i.e., habitat saturation). When saturation occurs, local density stabilizes, but population size can still increase through population expansion mediated by floaters (i.e., nonbreeding individuals) dispersal. These mechanisms rely on the assumptions that there are no density effects on territory size (i.e., territory compression) or on the costs of territorial defense. Consequently, there is no reduction in the suitability of the territories or in the fitness of already established individuals as the population grows (Rodenhouse et al. 1997). The demographic outcomes of populations regulated by these processes may differ from those predicted under the crowding approach. For example, social spacing due to territoriality might modify the demographic carrying capacity. Given the conflict over space use, equilibrium sizes of territorial populations are often lower than those lacking territorial defense (López-Sepulcre and Kokko 2005). These differences may be crucial in understanding patterns of herbivore abundance, spatial distribution, and resource use, while failing to account for departures from conventional models may misguide sustainable management initiatives (Festa-Bianchet 2007).

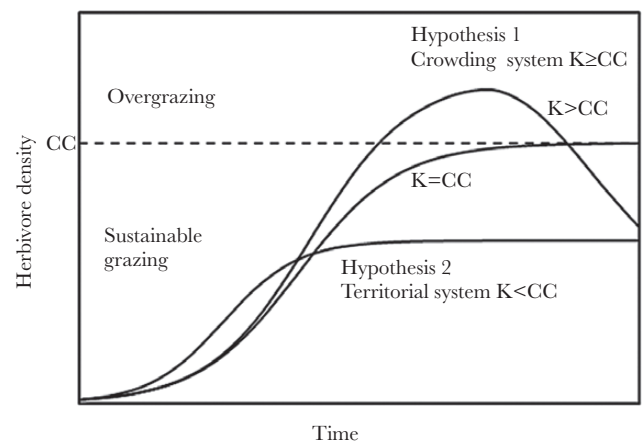
Although addressed in a wide range of taxa, including insects, birds, and small mammals (Rodenhouse et al. 1997), the potential role of territorial defense in the dynamics of large herbivores has rarely been considered. The aim of this study was to explore empirical evidence to test contrasting hypotheses about crowding

and resource defense as the potential mechanism driving the regulation of guanaco densities in wild populations from northeastern Patagonia. We evaluated a body of observational evidence on the relationship between guanaco demography and forage availability in the light of the different mechanisms of population regulation discussed above. The crowding hypothesis (hypothesis 1) would be supported if density effects on recruitment (1.1), mediated by food supply reduction (1.2), were detected. We focused on recruitment because, among ungulates, reproduction is the main target of limiting factors whereas adult mortality tends to be buffered against density effects (Gaillard et al. 1998). Within this scenario, density is expected to stabilize near the environmental carrying capacity predicted by an equal share of available forage (1.3). On the contrary, density limitation through territoriality (hypothesis 2) would be supported if recruitment remains density independent (2.1) and density effects on food supplies are not detected (2.2). Under this model, vital rates remain density independent because already established individuals and their territories are unaltered by population growth. Finally, if territorial behavior drives density regulation, equilibrium density is expected to remain below the environmental carrying capacity predicted by an equal share of available forage (2.3). Figure 1 outlines the conceptual models underlying each hypothesis.

## MATERIALS AND METHODS

### Study species

The guanaco is the only native ungulate inhabiting Patagonian deserts and semideserts. Its mating system is a resource-defense polygyny (Franklin 1983) in which territorial defense is a prominent feature influencing the spatial distribution of the individuals across the landscape (Raedeke 1979). The main social units in this system are family groups, composed by an adult male that defends a territory where a group of females with their offspring of the year (chulengos) forage; male groups, composed mainly of juveniles and adult males; and solo males (Franklin 1983). Both male and female yearlings are expelled from family groups by the territorial male, typically before and after the onset of the mating season (Franklin 1983; Bank et al. 2003). Male yearlings form new or add



**Figure 1**

Conceptual models representing crowding and resource-defense hypotheses. CC is the environmental carrying capacity, defined by the maximum number of animals that the environment can support sustainably;  $K$  is the demographic carrying capacity, defined by a null rate of population increase.

to the existing male groups whereas females do so to family groups (Franklin 1983). In our study location, a few yearling females or a mother with a yearling offspring have been occasionally observed in the large male groups, though their presence in these social units is clearly ephemeral. Individuals in male groups do not participate in reproduction and they are not territorial. In sedentary populations family groups remain in their territories year-round (Burgi 2005), whereas in migratory populations, all sex and age categories congregate in migratory mixed herds in late-fall/early winter a number of months after the mating season (Franklin 1983; Ortega and Franklin 1995). The population present in our study area is sedentary, and the average family-group size remained stable and density independent during the study (Marino and Baldi 2014). During the past century, overgrazing by domestic sheep (*Ovis aries*) has led to massive land degradation (Golluscio, Deregibus, et al. 1998), including severe desertification of nearly 30% of the 700 000 km<sup>2</sup> Patagonian steppe (Del Valle et al. 1998). The guanaco, the dominant native herbivore in this ecosystem, has been historically considered by ranchers as the only relevant competitor and a threat to livestock production. Although guanaco numbers have declined dramatically due to competitive exclusion by livestock, uncontrolled hunting, and land degradation (Baldi et al. 2006) during the last decade, local density has increased at some sites, exacerbating the guanaco-farmers conflict. Preventing overgrazing by guanacos is among the major arguments underlying imminent culling initiatives promoted by government agencies and Patagonian ranchers. In this context, to understand the factors involved in the regulation of guanaco densities and grazing impact, is crucial to plan adequate management regimes.

## Study location

This study was conducted in San Pablo de Valdés (San Pablo), which is located in Península Valdés (42°36'S; 64°15'W), Chubut Province, Argentina. In 2005, a local NGO purchased this 73 km<sup>2</sup> ranch formerly dedicated to sheep production, in order to convert it into a private wildlife reserve; all the circa 3500 sheep were removed and a permanent warden was appointed. San Pablo is delimited by 1-m-high wire fences, which restrict livestock movements from neighboring ranches. Guanacos are able to jump over these fences although they occasionally get entangled and die. For this reason, fences are considered semipermeable barriers to guanaco movements (Rey et al. 2012). The San Pablo population increased rapidly during the first years of the study (2006–2012), when marked immigration from neighboring ranches took place (Marino et al. 2014), increasing group density until 2012, when it reached a seemingly equilibrium point. The natural predator of guanacos, the puma (*Puma concolor*), is rare in Península Valdés (Nabte 2010) and predation risk during this study can be considered null. The other 2 species of medium-sized herbivores found at this location, the choique (*Rhea pennata pennata*) and the mara (*Dolichotis patagonum*), occur at extremely low densities when compared with guanacos to be considered relevant competitors. The major vegetation communities of San Pablo have been described elsewhere (Codesido et al. 2005; Burgi et al. 2012), and this study was conducted across 5 of them: 1) shrub–grass steppe, dominated by *Chuquiraga erinacea* var. *hystrix*; 2) grass–shrub steppe, dominated by *Sporobolus rigens*, *Nassella tenuis*, *Piptochaetium napostaense*; 3) shrub steppe, dominated by *Chuquiraga avellanadae*; 4) dwarf-shrub steppe, dominated by *Hyalis argentea*; and 5) grass steppe, dominated by *S. rigens* and *N. tenuis*.

## Data collection

Postreproductive surveys were conducted to assess spatial distribution, density, and population structure. In this region, the birth season typically starts in early November and extends to middle-late December. Surveys were conducted during January and February, except for 2008 when they were conducted on early April. The population of San Pablo has been surveyed every year from 2006 until 2014, except for 2007. Data collection was based on ground, line-transect surveys in which group sizes and composition, as well as other relevant data, were recorded. Approximately 22 km<sup>2</sup> were effectively sampled during these surveys, resulting in 30% of the reserve area. This effort was distributed along 3.7, 3.2, 7.6, 3.9, and 3.7 km<sup>2</sup> of vegetation community 1, 2, 3, 4, and 5, respectively. A detailed description of population surveys and criteria to assign groups to social categories is provided elsewhere (Marino and Baldi 2014).

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). Transects were placed across the 5 major vegetation communities present in the reserve, and both local (i.e., vegetation community specific) and global (i.e., entire reserve) density estimates were computed for every year of the data set. Density estimations were performed using *Distance 5.0* software (<http://www.ruwpa.st-and.ac.uk/distance/>). The chulengo:female ratio at a local and population level was computed by means of the number of chulengos and adult females recorded after every breeding season and was considered a measure of recruitment (Marino et al. 2014). Guanaco carcasses encountered during population and walking surveys, in addition to opportunistic records, were used to estimate carcass density and approximate survival rates for adults and chulengos during 2012 and 2013.

To account for the potential influence of interannual variation in primary productivity on recruitment across 2006–2014, we used the Enhanced Vegetation Index (EVI) derived from MODIS satellite images. Imagery processing is detailed elsewhere (Marino et al. 2014). The average value of the entire phenological cycle was used as a proxy of primary production for each year considered in the sample (Pettorelli et al. 2005).

Perennial grasses are guanacos' preferred forage in the area and are considered a key functional group in previous studies on guanaco foraging patterns (Baldi et al. 2004). In order to assess CC, we placed 34 vegetation enclosures (0.5 × 0.5 m) across the major vegetation communities of San Pablo. The enclosures were located in patches that were considered to be representative of the spatial heterogeneity of each vegetation community (7 cages per community). A year later, plant biomass inside the cages was harvested. Some enclosures were damaged or lost during the annual cycle, resulting in a sample size of 34, 32, and 26 in 2011, 2012, and 2013, respectively. The dried weight of edible grasses was used as an indicator of aboveground primary productivity of preferred forage per enclosure per year. We assessed preferred forage production per vegetation community extrapolating enclosures data and considered this measure as a proxy of preferred forage availability during 2011, 2012, and 2013.

Finally, we used data from the Vegetation Monitoring System that was established at the study area in 2009 in order to detect eventual changes and trends in vegetation structure and composition. This system consists of 4 fixed sampling sites (one per vegetation community) that are annually sampled following the MARAS

protocol (Spanish acronym standing for Environmental Monitoring of Arid and Semiarid Regions) (Oliva et al. 2006). Specific cover is assessed in 2 of the MARAS transects using the point-quadrat method, recording canopy interceptions with the pin (at plant species level) at intervals of 20 cm. In order to evaluate temporal changes in habitat quality, we used the data corresponding to cover of edible perennial grasses present at San Pablo. Plant communities 1, 3, and 5 have been annually sampled since 2009 resulting in 6 years of data, whereas community 4 monitoring began in 2011. So far, there has been no vegetation monitoring in community 2; therefore, we lack data on interannual variability in forage cover for this community. Guanaco groups were consistently observed foraging in the monitors' areas during the entire study.

### Statistical analyses

To assess the factors driving recruitment variation, we fitted linear models to the young:female data, at both local and population levels. The full model for local recruitment included the intercept and the terms vegetation community, local density, and the interaction between them. In order to account for the potential influence of interannual variation in primary productivity, we included the annual average of EVI values. The full model for recruitment at population level included the intercept and the terms population density and annual EVI. We also included a combination of both terms (EVI/population density) that has proven to be relevant in other settings (Marino et al. 2014). Model selection was based on Akaike information criterion (AIC), selecting a subset 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 (Crawley 2007).

In order to assess changes in grazing impact during population growth, we fitted a linear mixed model to the data on preferred forage cover obtained from the Vegetation Monitoring Program in communities 1, 2, 3, and 4. The full model for forage cover included the intercept and the terms vegetation community, local density, and the interaction between them. In order to account for the potential influence of climatic driven effects, we included annual rainfall estimates obtained from the closest meteorological station available, which is located 60 km westward from San Pablo (CENPAT-CONICET). Because the same transects were used every year to assess changes in grass cover, transect identity was included as a random term in order to account for the lack of independence between data obtained from the same transect (Crawley 2007). Serial autocorrelation was discarded by visual inspection of residual plots.

### Minimum environmental carrying capacity

To test for differences in productivity among vegetation communities, we fitted a linear model to the data on dry biomass of preferred forage obtained from the enclosures, which were log-transformed to account for variance heterogeneity. To test the hypothesis that a territorial system yields lower population sizes than those expected under the crowding model, we estimated the minimum CC expected under the crowding model by approximating the total availability of preferred forage in the study area. We estimated the annual forage production per surface unit within each vegetation community extrapolating enclosures data and then computing a global average production weighted according to effort distribution of population surveys across vegetation communities. We considered that guanacos could consume 50% of the annual forage production without exerting detrimental effects on the environment, as recommended by previous studies on

semicaptive guanacos (Von Thüngen 2003). Our operational definition of CC under the crowding model refers to the maximum number of adult guanacos that the available forage can support sustainably. San Martin and Bryant (1989) showed that South American camelids have adapted to the harsh environments that they inhabit by reducing intake and decreasing the transit time of digesta through the tract when compared with "advanced" ruminants, such as sheep or cattle. In the mentioned study, the authors reported a daily intake of 2% of body weight or lower for South American camelids under grazing conditions, in contrast to the 3% often cited for advanced ruminants or captive guanacos fed with alfalfa pellets (Von Thüngen 2003). Considering an adult body weight of 75 kg for males and nonpregnant females, and 110 kg for pregnant females (Von Thüngen 2003), an even sexual ratio and that half of the females in the population reproduce every year, we computed a weighted average of adult body weight of 85 kg. Therefore, we estimated the annual requirement of an adult guanaco to be 620 kg of dry biomass. In addition, it was assumed that a chulengo consumed one-third (0.34) of the forage required by an adult (Von Thüngen 2003) and a yearling required the same intake as an adult. We consider our local density data to be adequate to assess how gross changes in density would affect recruitment and vegetation performance because we expect our density estimates to be highly correlated with the relative grazing pressure that each community suffers throughout the year. However, the density determining the absolute grazing pressure, required to make comparisons with CC, would hardly be precisely estimated at local level by a single postreproductive survey. Approximately 20–30% of the population at equilibrium is congregated in nonterritorial male groups. These are a few large groups that wonder among vegetation communities, increasing instantaneous loads locally and changing location from 1 year to the next, in an unpredictable way. Therefore, the temporal resolution of our data precludes precise estimations of local density on an annual basis to be compared with local estimates of CC. However, the variation induced by the movement of nonterritorial groups is diluted when density is assessed at global scale because we are not making specific assumptions about where these individuals are foraging, we only consider that they are present in the global area. For this reason, we consider that the global level is the appropriate scale to test this hypothesis.

## RESULTS

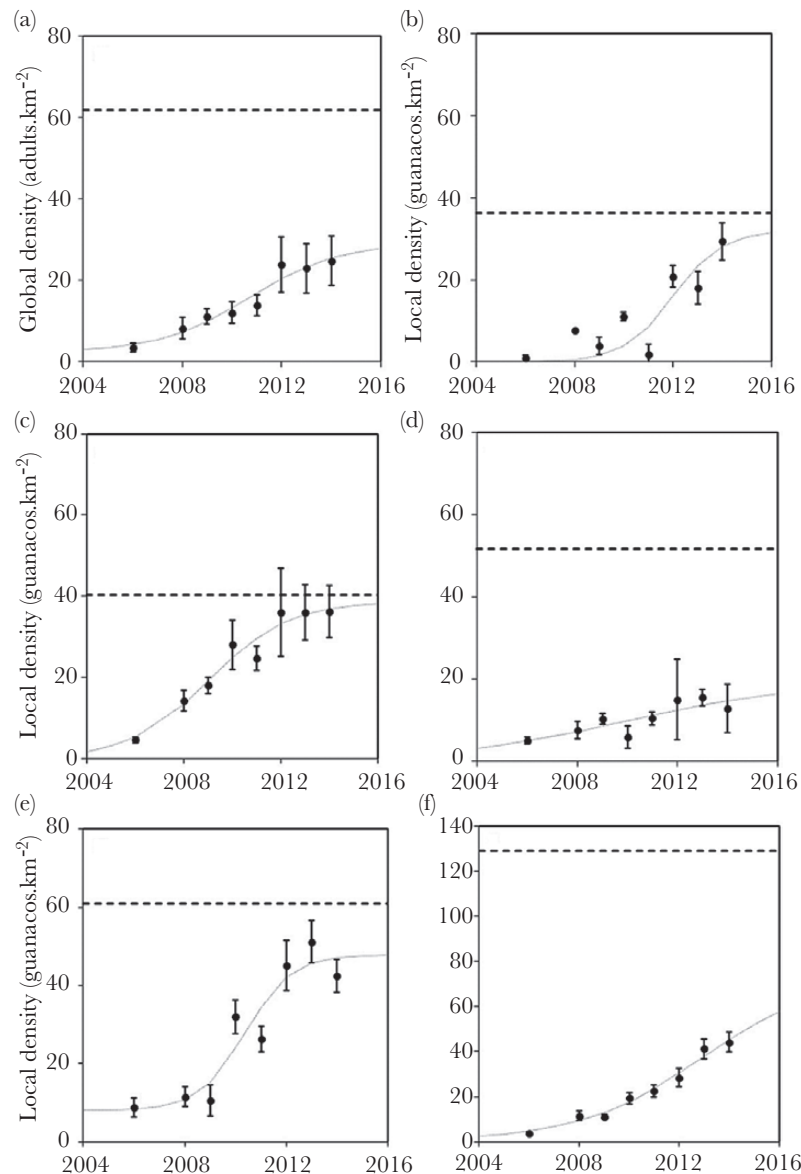
### Population growth

Guanaco density within San Pablo rose from 3.95 (standard error [SE] = 1.05) in 2006 to 26.3 (SE = 6.82) guanacos/km<sup>2</sup> in 2012, oscillating around 26.7 during the 2012–2014 period (Figure 2). The instantaneous rate of increase was negatively related to population density (delta AIC = -2.5 with respect to the null model; slope = -0.014; SE = 0.007;  $R^2 = 0.37$ ). Regarding the 2012 and 2013 surveys, survival rates were estimated in 97% for adults and 86–87% for chulengos, whereas we found no dead yearlings. The projection of the 2012 population, considering observed recruitment and survival rates and assuming no emigration, indicated that after 3 years, the guanaco density inside San Pablo would have to be 27% higher than the actual density observed in 2014 (predicted lambda = 1.14, observed lambda = 1.01), suggesting a significant exodus of individuals during the last years of the study.

### Heterogeneity in recruitment

The average chulengo:female ratio at global level was 0.53 with relatively low interannual variation (standard deviation [SD] = 0.08,





**Figure 2**

Guanaco densities throughout the study. (a) Global estimates converted to adult equivalents, to allow visual comparison with the global environmental carrying capacity (CC, represented by the dashed line). Local estimates of individual densities in (b) vegetation community 1; (c) vegetation community 2; (d) vegetation community 3; (e) vegetation community 4; (f) vegetation community 5. Error bars represent standard errors. Solid lines are intended for visual purposes only.

coefficient of variation = 15%). Regarding the local level, the chulengo:female ratio differed among vegetation communities (Table 1), being higher in richest habitats (Table 2), and was positively related to EVI (i.e., indicator of relative annual forage production). However, there were no significant effects of density on this response variable, at either local or population level (Table 1, Figure 3).

### Equilibrium density, demographic carrying capacity, and environmental carrying capacity

Preferred forage availability differed significantly among vegetation communities (Table 1), with richer communities producing 2–5 times more forage than poorer ones (Table 2). There were no statistical differences in forage production between the 3 years considered in this test (Table 1). The annual production computed for the study area was 76.7 tons/km<sup>2</sup> of preferred forage. The average population density

during the 2012–2014 period was 23.3 guanacos/km<sup>2</sup> expressed as adult equivalents (SD across years = 0.78), with the highest density observed of 24.2 ( $\pm 6.01$ ) adult guanacos/km<sup>2</sup> in 2014. We considered this average as the observed equilibrium density of our data set. The projection of the linear relationship between the instantaneous rate of increase and population density predicted a demographic carrying capacity ( $K$ ) of 31.6 guanacos/km<sup>2</sup>. All these values were lower than the CC predicted by an equal share of the 50% of annual forage production during 2011–2013, which was 61.8 adults/km<sup>2</sup> (95% confidence interval lower limit = 41.6 adults/km<sup>2</sup>).

### Vegetation performance

The observed differences in edible-grass cover among years were explained by interannual variation in rainfall whereas changes in guanaco density had no effect on this variable (Table 1). The

**Table 1**  
**Delta AICc scores used in model selection**

Model terms	Population recruitment	Local recruitment	Forage production	Vegetation performance
Intercept	8.37	12.8	34.4	32.1
I + vegetation community	—	4.16	0.00	12.7
I + local density	—	14.14	—	29.1
I + population density	14.0	—	—	—
I + annual EVI	0.00	9.58	—	—
I + year	—	—	37.7	—
I + annual rainfall	—	—	—	19.32
I + vegetation community + local density	—	6.40	—	11.23
I + vegetation community × local density	—	10.72	—	20.4
I + vegetation community + year	—	—	1.59	—
I + vegetation community × year	—	—	6.16	—
I + vegetation community + annual EVI	—	0.00	—	—
I + vegetation community + annual EVI + local density	—	2.32	—	—
I + vegetation community × local density + annual EVI	—	8.97	—	—
I + annual EVI + local density	—	11.32	—	—
I + annual EVI + population density	3.18	—	—	—
I + annual EVI. Population density <sup>-1</sup>	13.2	—	—	—
I + vegetation community + annual rainfall	—	—	—	0.00
I + annual rainfall + local density	—	—	—	22.0
I + vegetation community × annual rainfall	—	—	—	8.89
I + vegetation community × local density + annual rainfall	—	—	—	6.24
I + vegetation community + annual rainfall + local density	—	—	—	3.16
I + vegetation community × annual rainfall + local density	—	—	—	12.6
I + vegetation community × (annual rainfall + local density)	—	—	—	11.5

EVI, Enhanced Vegetation Index; I, intercept.

**Table 2**  
**Model parameters and predicted values<sup>a</sup>**

Vegetation community	Local recruitment (chulengo:female ratio)		Preferred forage availability		Cover of preferred forage through 2009–2014	
	Estimate (SE)	Predicted recruitment <sup>b</sup>	Estimate (SE)	Predicted biomass (kg/ km <sup>2</sup> /year)	Estimate (SE)	Predicted % <sup>c</sup>
1 (Intercept)	−0.353 (0.280)	0.371	1.685 (0.121)	44 900	23.4 (6.5)	44.4
2	0.095 (0.064)	0.467	0.109 (0.222)	50 100	—	—
3	0.136 (0.064)	0.507	0.353 (0.176)	64 000	−8.3 (6.5)	36.1
4	0.271 (0.064)	0.642	0.520 (0.176)	75 600	15.5 (7.0)	60.0
5	0.131 (0.064)	0.502	1.270 (0.213)	159 900	61.6 (6.6)	100.0
Annual EVI (slope SE)	5.920 (2.235)	—	—	—	Annual rainfall (slope SE)	0.131 (0.03)

EVI, Enhanced Vegetation Index.

<sup>a</sup>Model parameters are expressed as differences with respect to the intercept (i.e., reference level), which is vegetation community number 1.

<sup>b</sup>Predicted recruitment was computed considering an average annual productivity of 0.1206 EVI units.

<sup>c</sup>Predicted forage cover was computed considering an average annual rainfall of 160 mm.

average cover of edible grasses differed among plant communities, with an average cover of 40% in the relative poor shrublands and 100% in the richest grassland (Table 2).

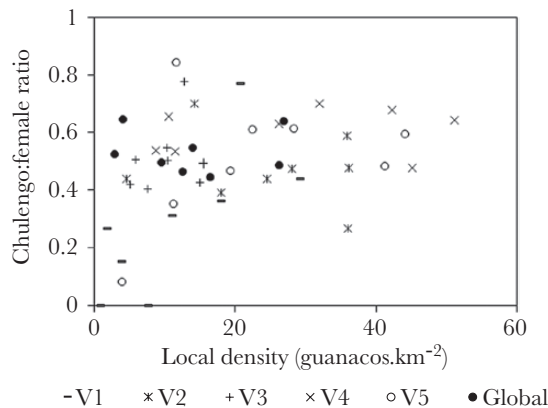
## DISCUSSION

### Regulation of population density

After the implementation of the reserve, guanaco density inside San Pablo exhibited drastic changes, increasing rapidly during the first years then stabilizing around a seemingly equilibrium point. The observed decrease in the instantaneous growth rate at global level indicates that some regulatory process was operating on population density during the last stages of the study. The inter-annual variability in the chulengo:female ratio was relatively low and remained density independent along the population trajectory; thus, changes in reproductive rates are unlikely to be responsible for the observed pattern in guanaco numbers. However, the lack

of data on individual performance prevents us from discarding the potential effects of age–structure changes on recruitment that may mask density dependence, such as those observed operating on survival rates in other ungulate species (Festa-Bianchet et al. 2003). Thus, recruitment patterns must be considered with caution until additional information confirms our findings. The lack of density effects on guanaco recruitment at local scale and the fact that equilibrium density remained below the environmental carrying capacity predicted by an equal share of the available resources denies crowding as the mechanism regulating guanaco density in the study area. The absence of density effects on edible-grass cover and recruitment at both local and population levels is in agreement with the hypothesis of density limitation through territorial defense.

Previous studies on guanacos have reported density dependence in population abundance (Raedeke 1979; Zubillaga et al. 2014), but the mechanisms underlying these patterns are still uncertain. For example, a negative correlation between guanaco birth mass



**Figure 3**

Observed recruitment at global (population) and local (vegetation community specific) levels, as a function of postreproductive population density from 2006 to 2014.

and population density was found in the migratory population of Torres del Paine, Chile (Sarno and Franklin 1999); however, juvenile survival in the same population seems to remain density independent (Sarno et al. 1999). Although it is implicitly assumed that crowding regulates guanaco densities across Patagonian rangelands (Rabinovich and Zubillaga 2011), empirical evidence of crowding effects on vital rates has only been reported in a very small population, Cabo Dos Bahías Reserve, which is surrounded by the sea in most of its perimeter (Marino et al. 2014). Within this small reserve, environmental variability coupled with density dependence shapes recruitment and survival rates, and occasionally promotes important population fluctuations. This atypical dynamic for a guanaco population is in accordance with the expected emergence of crowding effects in territorial species if dispersal capability is reduced (Rodenhouse et al. 1997), which has been suggested to be the case in this reserve (Baldi et al. 2006; Marino et al. 2014). Thus, the emergence of striking crowding effects in this partially confined population reinforces the idea of resource defense as the mechanism limiting density in populations with regular dispersal capability, such as the one observed in our study area.

Territorial defense is considered among the intrinsic self-regulatory mechanisms that reduce population growth before the effects of resource limitation become evident and has been shown to be an important regulatory agent in different taxa, including insects, fish, reptiles, birds, and small mammals (Wolff 1997; López-Sepulcre and Kokko 2005). However, the debate regarding large herbivores regulation has been focused on top-down versus bottom-up processes, assuming that the influence of territory-based social spacing is negligible in this group (Krebs 2009; Sinclair et al. 2010). This omission may be founded on the assumption that ungulates are nonterritorial animals (Wolff 1997) or on the fact that territorial defense is rare among northern ungulates (Franklin 1983; Flueck 2000). Instead of a third type of regulation, we consider density limitation in resource-defense polygyny ungulates as a special case of bottom-up regulation in which primary productivity and defense costs interact to determine territory size and hence population density. This idea is supported by studies addressing the inverse relationship between guanaco territory size and preferred forage productivity (Franklin 1983).

Under the hypothesis of limitation through territorial defense, recruitment and survival are expected to remain density

independent, whereas dispersal is expected to regulate population density. Unfortunately, we were not able to assess dispersal rates directly due to the lack of tagged individuals in the population. However, indirect evidence seems to support the proposed mechanism. The difference between guanaco densities at San Pablo and those predicted by a theoretically closed population projected using the observed recruitment and survival estimates during the latest years of the study suggests an important exodus of individuals from the study area. This result is consistent with the idea of forced emigration of floaters after saturation of available territories under the resource-defense system. In the case of the vicuña (*Vicugna vicugna*), which is the other species of South American wild camelids and shows a mating system and social organization similar to those of sedentary guanacos, Franklin (1974, 1983) found that family-group size was regulated by forced dispersal of both male and female juveniles and the typical nonacceptance of new adult females into the group by the territorial male. As a consequence, at the end of each annual cycle, the local density was relatively constant while, after a saturation threshold was reached, the total surrounding population increased by the spilling over into the unoccupied habitats (Franklin 1974, 1978). This mechanism of density limitation and population expansion is in agreement with the one we have proposed for the guanaco population in our study area. Therefore, we can hypothesize that density dependence, which typically operates through reproduction rates among ungulate species (Gaillard et al. 1998), shifts to dispersal rates under the territorial system observed in San Pablo. The idea of density-dependent dispersal as a major agent regulating guanaco densities is consistent with both the striking immigration reported for these and other populations before saturation is reached (Marino et al. 2014) and massive movements between management units triggered by drastic changes in livestock loads (Raedeke 1979; Baldi et al. 2001). Further research on individual performance and direct observations of individual movements will allow for testing this hypothesis at pertinent spatial scales and assessing the relative importance of dispersal to regulate herbivore densities under resource-defense systems.

### Demographic versus environmental carrying capacity

Previous studies have assessed  $K$  as an outcome of territorial conflict showing that territoriality often yields lower population sizes than a nonterritorial system (López-Sepulcre and Kokko 2005). Our results are in accordance with this finding, suggesting an equilibrium density under the territorial scheme that is bounded by behavioral constraints below the one predicted by forage availability. We have underestimated forage availability by ignoring edible shrubs and highly nutritious forbs, although these items were 28–47% of guanaco diet at San Pablo (Marino A, unpublished data) and important components when grasses are senescent or less available (Raedeke 1979; Baldi et al. 2004). For these reasons, we have referred to our estimate of forage (grasses) availability as the minimum CC. However, although we used the plant species with highest forage value for CC calculation, we did not evaluate eventual energetic limitation, an issue that should be explored. Nevertheless, we expect the actual difference between the observed density and the one predicted by the sole forage availability to be even larger than the one we reported here, reinforcing our conclusions. Regarding other ungulates, Bonacic et al. (2002) found that the density of a recovered vicuña population unexpectedly stabilized below the environmental carrying capacity predicted under a crowding model. This result

supports the idea of territorial defense limiting density in another species with a similar mating system.

The major limitation of our study is the relatively short length of the time series for a large mammal such as the guanaco. Although we have not made specific predictions about local occupation patterns, it is not clear if local density in vegetation communities 1 and 5 has reached an asymptote. Vegetation community 1 holds the only permanent water source in the reserve thus, depending on the season, weather and the time of the day, numerous male groups, and family groups may be seen in this community, even if their territories or feeding areas are somewhere else. This fact may explain the great variation in local density observed which presumably mask the actual occupation pattern. According to the low forage availability and the low density values intercalated in the time series, it is likely that the permanent density in community 1 to be relatively low rather than high. On the other hand, guanaco density within vegetation community 5 seems to be still increasing. Community 5 is the more productive habitat and holds the highest local density in the reserve. An exploratory projection of this time series suggests that local density could reach an approximate  $K$  of 70 adults/km<sup>2</sup> within 10 additional years of population growth. Forage availability within community 5 suggests that even a density as high as that would not be enough to consume 50% of available biomass. Our global results may also change according to future increments in this community. However, community 5 represents only 16% of our study area and even with an increase as large as 40 additional adults/km<sup>2</sup>, the effect on the global density would be an increase of 6.4 adults/km<sup>2</sup>. Since even with this increment, global density would be well below the global environmental carrying capacity, it is unlikely that our conclusions change as a result of the probable increments of local density within community 5.

The crowding model predicts a progressive decrease in resource availability (i.e., food exhaustion) as the population approaches the carrying capacity. In contrast, under territorial-based mechanisms, density-independent outcomes for forage availability within already occupied territories are expected along population trajectory. Thus, the absence of density effects on grasses cover assessed by the Vegetation Monitoring Program at San Pablo also supports the hypothesis of density limitation through territoriality. After accounting for interannual rainfall variability, preferred forage cover did not exhibit substantial changes from 2009 to 2014, regardless of the 2-fold increase and stabilization of guanaco density. Since livestock removal in 2005, the previously overgrazed vegetation has shown noticeable improvements in terms of cover of edible plants and biodiversity, among other indicators of conservation status (Burgi et al. 2012). This lack of herbivore-density effects on forage availability in a recovered rangeland is among the first empirical contributions to the study of the grazing impact by free-ranging guanacos. Other herbivore studies have shown that territorial defense lowers the maximum density of animals that can coexist and hence lowers the maximum disturbance rate over vegetation resources (Nevo 1979; Gordon and Lindsay 1990; Seabloom and Reichman 2001; Seabloom and Richards 2003). We hypothesize that density limitation below the environmental carrying capacity in populations of wild South American camelids with regular dispersal capability prevents overgrazing, and may buffer population fluctuations in these highly variable environments. The results reported by Shaw et al. (2012) in which the numbers of a recovered vicuña population remained fairly constant instead of fluctuating as greatly as their model predicted according to rainfall variability,

are consistent with this idea. Future monitoring will allow confirming the long-term stability of the global density pattern and the vegetation performance observed in this study.

## Conservation and management implications

At present, ranchers concerns and overgrazing risks exhort culling initiatives aimed at hindering the perceived guanaco overpopulation in Patagonian rangelands. Although recent studies suggest that guanaco impact on plant community is lower than that of domestic sheep (Burgi et al. 2012), and grazing impact by domestic and wild herbivores across productive lands is often confounded, guanaco harvest quotas in Argentinean Patagonia are derived from classic models that ignore these facts and oversimplify guanaco dynamics. Those models assume a demographic carrying capacity equivalent to an environmental carrying capacity that is set by forage availability once livestock load has been accounted for. According to this classic crowding approach, per capita food supply is computed by estimating available forage for sheep and dividing it among both species according to body weight equivalents (Rabinovich and Zubillaga 2011) but without any other consideration on the relative grazing impact, intake rate, or efficiency. Density dependence is supposed to operate on reproductive rates in a logistic-like manner (Rabinovich and Zubillaga 2011), and guanaco populations within single ranches are implicitly supposed to behave as closed demographic units. Our findings contradict many of these assumptions. This study is the first empirical evidence on the mechanism driving guanaco regulation while accounting for vegetation dynamics, challenging the extent of the current assumption of crowding as the mechanism shaping guanaco densities across the region. Our results suggest that territorial defense by guanaco males acts as a regulating agent of population density, buffering crowding effects, and preventing vegetation depletion, opposing northern herbivores behavior. Actually, it has been suggested that it was the absence of a self-regulating mechanism such as territoriality, the reason why northern cervids exerted such a negative impact on biodiversity (Flueck 2000). Although further research is required to assess the scope of our conclusions, this mechanism that allows guanacos to self-adjust population density to resource availability before a detrimental grazing impact is inflicted, challenges the need of intervention in the sake of vegetation integrity within permeable-fenced protected areas. Moreover, our results stress the need to search for empirical support to the overabundance assumption that drives current culling initiatives in private lands, where sustained livestock overload and inadequate sheep distribution has proven to be the major agent responsible for habitat degradation (Golluscio, Giraud, et al. 1998; Ares 2007; Andrade 2012).

According to our findings, other factors in addition to food availability may determine the demographic carrying capacity under resource-defense systems, stressing the importance of accounting for behavioral traits when addressing population regulation and management issues. This combined approach, which takes into account behavioral, demographic, and vegetation perspectives, may contribute to the understanding of the processes shaping herbivore distribution and grazing impact across the landscape.

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