

Ecological drivers of guanaco recruitment: variable carrying capacity and density dependence

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Abstract Ungulates living in predator-free reserves offer the opportunity to study the influence of food limitation on population dynamics without the potentially confounding effects of top-down regulation or livestock competition. We assessed the influence of relative forage availability and population density on guanaco recruitment in two predator-free reserves in eastern Patagonia, with contrasting scenarios of population density. We also explored the relative contribution of the observed recruitment to population growth using a deterministic linear model to test the assumption that the studied populations were closed units. The observed densities increased twice as fast as our theoretical populations, indicating that marked immigration has taken place during the recovery phase experienced by both populations, thus we rejected the closed-population assumption. Regarding the factors driving variation in recruitment, in the low- to medium-density setting, we found a positive linear relationship between recruitment and surrogates of annual primary production, whereas no density dependence was detected. In contrast, in the high-density scenario, both annual primary production and population density showed marked effects, indicating a positive relationship between recruitment and per capita food availability above a food-limitation threshold. Our results support the idea that environmental carrying capacity

fluctuates in response to climatic variation, and that these fluctuations have relevant consequences for herbivore dynamics, such as amplifying density dependence in drier years. We conclude that including the coupling between environmental variability in resources and density dependence is crucial to model ungulate population dynamics; to overlook temporal changes in carrying capacity may even mask density dependence as well as other important processes.

Keywords Ungulates · Herbivore dynamics · Food limitation · Environmental variation · *Lama guanicoe*

Introduction

Identifying the factors shaping variation in vital rates is essential to understand the processes that limit populations. Under the traditional pattern-orientated approach, ecologists try to infer the operating mechanisms from the analysis of time series of population size. In recent years, several studies have shown that analyzing relationships between vital rates, density and climatic variables may detect important processes influencing population dynamics that time series methodologies may overlook (Coulson et al. 2000; Gaillard et al. 1998; McCullough 1999). It has been suggested that in order to understand demographic mechanisms, the process-orientated analyses of vital rates should be used to construct population models and the dynamics these models generate should be compared with observed dynamics described by pattern-orientated methods (Coulson et al. 2000). This combination of pattern- and process-orientated approaches has been particularly helpful to understand the way vital rates and population dynamics are associated with density-dependent and density-independent

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processes operating on large herbivore populations (Coulson et al. 2000).

Population dynamics of large herbivores can be strongly affected by a combination of stochastic environmental variation and density dependence (Gaillard et al. 1998; Pierce et al. 2012). These effects might be particularly evident in temperate systems where inter-annual variation in weather conditions is more pronounced than in lower latitudes. This is the case of many arid systems where water is the limiting factor to primary productivity and food availability for herbivores is determined mainly by rainfall (Noy-Meir 1973). In these desert and semi-desert environments rainfall is often variable and unpredictable, and periods of relatively high productivity alternate with poorer years and, occasionally, with drought events leading to very low forage production. As a result, environmental carrying capacity (i.e., maximum population density that a particular environment can support) can differ a lot from one year to the next and this variation is expected to affect herbivore dynamics (Bonenfant et al. 2009; Pierce et al. 2012; Shaw et al. 2012). To understand how this variation in forage productivity interacts with density dependence to affect vital rates it is crucial to address plant–herbivore dynamics and to develop adequate management programs. However, density effects are often hard to detect unless the studied population is close to ecological carrying capacity, where density dependence is highest. Moreover, different vital rates may respond differentially to density effects (McCullough 1999). For example, in large herbivores, recruitment is the main target of limiting factors, both density dependent and density independent, whereas adult mortality tends to be buffered against density effects (Bonenfant et al. 2009; Gaillard et al. 2000). Therefore, to study how density and environmental variation affect recruitment appears to be a promising first step to test hypotheses about processes limiting herbivore numbers.

Among ungulate species, population dynamics are particularly difficult to study because a long generation time requires long and systematic time series data which are often unavailable. Populations with contrasting densities but under comparable environmental conditions can help us to understand the relationship between density and vital rates when long time series are lacking. In particular, wildlife reserves located in areas where ungulates occur but predators have been extirpated offer the opportunity to study the effects of food limitation on population growth without the interference of potentially confounding factors, such as predation, hunting, or competition with livestock. The aim of this study was first to identify ecological factors driving inter-annual variation in guanaco (*Lama guanicoe*) recruitment at two predator-free reserves in eastern Patagonia with contrasting density scenarios; we tested the hypothesis that the combination of population density and

weather conditions affects guanaco recruitment through its effects on per capita forage availability. Explicitly, we hypothesized that as a result of variability in weather conditions, carrying capacity fluctuates over time. Our main expectation was that recruitment was positively related to per capita food availability through the combined effects of density dependence and inter-annual variation in primary production. The alternative hypotheses were that density dependence alone or climate alone would be the major factors explaining variation in recruitment. Secondly, we assessed the extent to which the observed recruitment may account for the growth experienced by each of the populations in order to verify the assumption that they behave as closed demographic units. In this regard, we expected the population growth rate predicted by the observed recruitment to be consistent with the actual growth rate.

Materials and methods

Study species

The guanaco is a medium-size herbivore (80 kg) and is the only native ungulate inhabiting Patagonian deserts and semi-deserts (Franklin 1983). Demographic studies on guanacos are scarce and available data on vital rates derive from studies on guanacos in captivity or from wild populations in a few locations (Cévoli 2005; De Lamo and Saba 1990; Fritz 1985; Puig 1986; Raedeke 1979; Sarno et al. 1999; Sarno and Franklin 1999). Guanacos can live up to 14 years in captivity (Amaya and von Thüngen 2001) but most females do not live beyond ten years of age in the wild (Franklin and Fritz 1991; Raedeke 1979). Females may not breed until 3 years of age and they only produce one chulengo (i.e., offspring) after 11.5 months of gestation (Raedeke 1979). Birthing in Patagonia occurs on late spring–early summer and overlaps with the mating season. The guanaco mating system is a resource defense polygyny and the social organization is highly structured (Franklin 1983). Main social units are family groups, composed of an adult male that defends a territory where a group of females with their offspring of the year forage; bachelor groups, composed mainly of juveniles and adult males; and solo males. In sedentary populations family groups remain in their territories all year round (Burgi 2005), whereas in migratory populations all sex and age categories congregate in migratory mixed herds after the mating season (Franklin 1983).

Study locations

San Pablo de Valdés ranch (San Pablo) is located in the southern portion of Península Valdés, Biedma department

Table 1 Summary of population attributes at Cabo Dos Bahías (C2B) and San Pablo (SP)

Location	Recruitment (SD)	Population density range (SE)	Annual EVI (SD)	Spring EVI (SD)	Annual rainfall (SD)
C2B ($n = 8$)	0.44 (0.23)	46.4 (9.24)–71.2 (17.8)	0.1311 (0.01)	0.1405 (0.02)	208.0 (50.1)
SP ($n = 7$)	0.52 (0.07)	3.95 (1.05)–26.3 (6.82)	0.1182 (0.01)	0.1262 (0.01)	148.3 (43.4)

Shown are the average recruitment SD, range of population densities observed during the recruitment sampling period, SE of density estimation, average annual and spring enhanced vegetation index (EVI), and average annual rainfall

n Sample size (number of years observed)

in Chubut province (42°36'S; 64°15'W). The most distinctive climatic factor across the peninsula is the low average annual rainfall (280 mm), which falls mostly in the autumn and winter. A detailed description of the vegetation communities can be found in Burgi et al. (2012) but on a general basis, they are composed of shrublands and grasslands typical of the Patagonian province (Codesido et al. 2005). In 2005, a local non-governmental organization purchased this 7,360-ha ranch, which was formerly dedicated to sheep production, for conversion to a private wildlife reserve; all the ca. 3,500 sheep were removed and a permanent warden appointed. After the drastic changes in management, the guanaco population has been increasing a lot (Burgi et al. 2012), from 3.95 (± 1.05) in 2006 to 26.3 (± 6.82) guanacos km^{-2} in 2012. Guanaco predators, pumas (*Puma concolor*), are very rare in Península Valdés (Marcela Nabte, personal communication) and predation risk inside the reserve can be considered null.

Cabo Dos Bahías is a small wildlife reserve (1,700 ha) located in the Ameghino department, southeastern Chubut (44°55'S; 65°31'W). The vegetation in this area is characteristic of the Patagonian province and composed of shrublands and grasslands. Shrublands are characterized by *Chuquiraga avellanadae* and *Lycium chilense*, and grasslands by *Stipa tenuis* and *Poa ligularis* (Beeskow et al. 1987). Average annual precipitation is 250 mm (Beeskow et al. 1987). There have been no reports of guanaco predators in the area for more than 20 years (provincial wardens, personal communication). During winter 2000, an extensive guanaco die-off occurred in Cabo Dos Bahías resulting in the death of more than 80 % of the population. Deaths were attributed to emaciation and inanition (Beldomenico et al. 2003). The following year, post-reproductive density was 9.01 (± 2.2) guanacos km^{-2} (Cévoli 2005), and subsequently the population showed a marked increase, reaching 71.2 (± 17.9) in 2008 and fluctuating around 60 (± 9.4) guanacos km^{-2} until present. Therefore, both locations showed important changes in population density during the study. However, in relative terms, San Pablo has increased from a low-density to medium–high-density level (Burgi et al. 2012), whereas Cabo Dos Bahías' density during our recruitment sampling (2005–2012) has varied around the highest values reported for a wild guanaco population (Table 1).

Both reserves are 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 semi-permeable barriers to guanaco movements (Rey et al. 2012). The diet of the guanaco in both reserves is similar, with highly preferred grasses such as *Poa* sp. and *Stipa* sp., and *Chuquiraga* sp. as main items among shrubs (A. Marino, unpublished data). There is no supplemental feeding or any type of intrusive management regarding herbivores or plant communities in either site. The other two species of medium-sized herbivores found at these locations are a flightless bird, the choique (*Rhea pennata pennata*), and a large rodent (8 kg), the mara (*Dolichotis patagonum*). Both species occur at extremely low densities when compared to guanacos, as in most of their distribution range (Alonso Roldán 2012; Pirronitto 2011). Domestic sheep (*Ovis aries*) from neighboring ranches enter occasionally into the reserves but are rapidly removed by wardens or ranchers. Hence, we assume that there is no interspecific competition affecting guanacos in our study locations.

Data collection

Post-reproductive surveys were conducted in both reserves to assess population density and recruitment. The data series are incomplete as post-reproductive surveys have not been performed every year. Since the Cabo Dos Bahías population collapsed in 2000, population density has been estimated in 2001, 2004 and every year from 2006 to 2012. San Pablo was surveyed every year from 2006. Except for the Cabo Dos Bahías' 2001 and 2004 surveys, and the 2007 survey in San Pablo, the number of young and adult females was recorded after every breeding season (January–February), including those born in spring 2012. Thus our recruitment data consist of 8 years of herd counts at Cabo Dos Bahías and 7 years at San Pablo. Data collection was based on ground line transect surveys conducted along available dirt roads (a total of 22 km of available roads at San Pablo and 10 km at Cabo Dos Bahías). During these surveys, two observers standing in the back of a pick-up vehicle scanned the surroundings searching for guanaco

groups. For every group encountered we stopped the vehicle and recorded group size and, whenever possible, group composition in terms of sex and age categories. We also measured the distance and azimuth from the transect line to the location where the group was standing when detected, using a laser range finder, as well as the azimuth from the transect line orientation, and the vehicle geographic location using a global positioning system.

Guanacos younger than 6 months and yearlings can be recognized easily but adult females and adult males are very similar. However, behavioral studies in the area have shown that during summer, the guanaco social organization is highly structured by territorial males (Marino 2012) and the recognition of social units can be used to estimate the number of females present. The main social units are family groups, bachelor groups and solo males. Bachelor groups are composed mainly of adult and juvenile males whereas family groups are composed of an adult male and a variable number of females with their offspring of the year (Franklin 1983). Therefore, if a group can be determined as a family, the number of adult females can be derived from the number of adults present. Recognizing family groups is easy when young guanacos are present but can be difficult when they are absent. In this case, a group corresponded to a family when the gender of more than 50 % of its members could be assessed and only one adult male was present among them. In every case, these observations were consistent with behavioral displays and spatial distribution of social categories which usually use different ranges. The groups without young that were too far apart to assess group composition were not considered in our analysis. Under these criteria it is possible that the number of females was underestimated; however, as undetermined groups are often small (from two to four individuals) and represent less than 5 % of the observed social units, we do not expect this error to be important. Recruitment was estimated by young:female ratios in late summer. Our operational definition of recruitment refers to the proportion of adult females with young out of the total number of adult females present in the sample, recorded 4–6 months after the onset of the birthing season. Although the young:female ratio may be unreliable in forested areas, it can be a useful proxy of ungulate recruitment in open habitats, such as the Patagonian steppes, where the detection probability of young is high (Bonenfant et al. 2005). In most occasions, population surveys were repeated twice or three times on successive days and recruitment estimates were averaged across days, unless adverse weather conditions (high wind speed or rain) and doubtful low detection of young prevented us from including that particular date in the annual estimate. During harsh weather young guanacos tend to lie down close to shrubs, making their detection difficult. In these cases, only data recorded under good weather were

considered to be reliable. The among-day variation in recruitment estimations (i.e., sampling variation) was relatively low, with an average coefficient of variation of 10 %, ranging from 8 to 12 %.

Estimating population density

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, 2006). Radial distances and azimuths recorded were used to estimate the perpendicular distance from the transect line to each observed group. By fitting a detection function to the distance data, an effective strip width can be estimated which, in addition to average cluster size and encounter rates, is used to estimate population density (Buckland et al. 1993). In order to reach the minimal sample size required to fit the detection function and to obtain representative measures of population density (i.e., account for the potential effect of adverse weather that may alter survey outcomes), whenever possible surveys were conducted twice or three times on successive days. Data from repeated transects were pooled and referred to the total effort along that transect to minimize data dependence and to obtain a reliable measure of encounter-rate variability (Buckland et al. 1993). Although the same transects were used in every survey, density was estimated independently for each year (i.e., only data collected in a given year were used to estimate annual population density). Therefore, if any change in detection probability has occurred during the study we expected it was accounted for by the particular detection function fitted that year, without relevant consequences for our results. Because surveys are restricted by road availability, estimates of population density refer to the areas covered by the surveys and extrapolations to the entire reserves must be considered with caution. Because both populations are largely composed of family groups (Marino and Baldi 2014) that are highly territorial and often spatially segregated from bachelor groups (Franklin 1983; Raedeke 1979) we do not expect our data to be biased by guanacos' movements between surveyed and non-surveyed areas. Densities were estimated using Distance 5.0 software (<http://www.ruwpa.st-and.ac.uk/distance/>).

Indicators of relative forage availability

To account for inter-annual variation in food availability, the enhanced vegetation index (EVI) derived from 250-m Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images was used as an indicator of primary productivity (Reed et al. 1994). These data are distributed by the Land Processes Distributed Active Archive Center (LP

DAAC) (lpdaac.usgs.gov). EVI is an enhanced version of the normalized difference vegetation index for which canopy background noise and residual aerosol influences are minimized (Pettorelli et al. 2005), and has been shown to be adequate to model Patagonian steppe dynamics where vegetation cover is relatively low (Mohr Bell and Siebert 2008). The entire phenological cycle was indexed for each year of the study period. Each MODIS image is the result of a 16-day composite in which only the higher quality, cloud-free, filtered data are retained for compositing in order to extract a single representative value for each pixel over the particular 16-day period (Solano et al. 2010). Therefore, we processed a sequence of 23 images for each year between 2005 and 2012. Quality assessment of imagery data was performed by overlapping EVI data with the pixel reliability layer available in MODIS land products. This layer provides a rank that captures overall pixel quality (NASA LP DAAC 2013). Only reliable pixels were considered for the analysis. Low-quality pixels were usually located near the coast and consisted of mixed pixels (i.e., water and land). For this reason the shoreline was intentionally avoided in our analyses (Pettorelli et al. 2005). From a total of 184 processed granules, only five affecting Cabo Dos Bahías and three affecting San Pablo had to be removed from the data set because the information corresponding to the entire area was corrupted. The total area covered by the population surveys was assumed to be 2 km from the transect line, except for some portions that were too close to the coast and were removed to avoid noisy data. We considered that the area near transects provides a better representation of foraging grounds used by observed family groups than the area occupied by the entire reserves. Road distribution is often determined by specific habitat features, such as canyons, dunes or rock outcrops, that might have primary production and herbivore density correlates. Although EVI values derived from surveyed areas were consistent with those obtained from the entire reserves, we considered that with this restriction we minimized the risk of erroneously extrapolating population density and recruitment estimates to zones that we were unable to survey, and of relating actual observed groups to misleading foraging ranges. Based on territory sizes recorded in a much poorer location (Burgi 2007) and local group densities, we assumed that the area considered to estimate primary productivity includes a representative sample of the territories used by observed family groups. These areas, corresponding to 53 and 45 % of Cabo Dos Bahías and San Pablo total area, respectively, were digitalized within a geographical information system (GIS) and overlaid with EVI images, using ArcGIS 10.0 software. Reliable EVI pixels inside these areas were extracted and averaged, obtaining a mean value for each location every 16 days. The annual sequence, beginning in January (the driest month), was

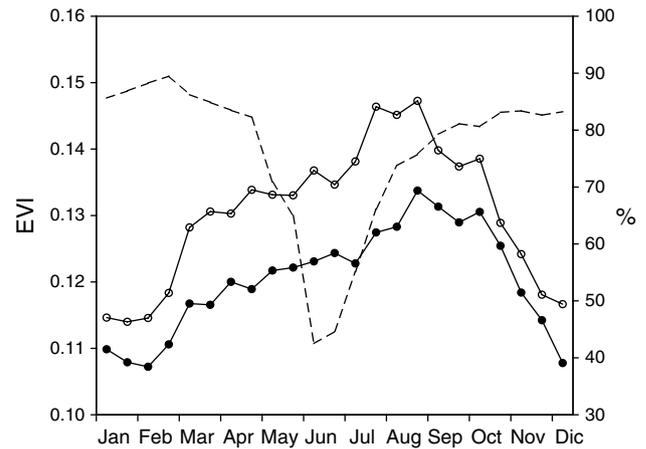


Fig. 1 Average enhanced vegetation index (EVI) annual cycle at Cabo Dos Bahías (empty circles) and San Pablo (filled circles). Data points are average EVI estimates corresponding to each particular 16-day composite across the 8 years of the study. The dashed line represents the average percentage of good-quality data found in the granules obtained on that particular date of the year

used to obtain two metrics as indicators of relative forage availability. The integral of EVI with respect to time provides an estimate of gross primary production (Tucker and Sellers 1986). Thus the EVI annual mean, that is supposed to be linearly related to above-ground primary production (Jobbágy et al. 2002; Pettoelli et al. 2005), was used as an indicator of overall annual productivity (Alcaraz-Segura et al. 2009). In northeastern Chubut, perennial grasses—the guanacos preferred forage—concentrate phenological activity in the winter–spring period, flowering in mid-spring and showing maximum leaf senescence in summer (Campanella and Bertiller 2008). Therefore, spring months are critical for female guanacos due to the occurrence of the greening peak of their preferred forage simultaneously with the high nutritional demands of late gestation. We considered the average EVI from the period between early August and early November as a measure of the spring primary production and forage availability during this crucial stage. Date selection was based on visual assessment of the average phenological cycle across the 2005–2012 period (Fig. 1). This cycle was constructed by averaging EVI values of each date specific 16-day composite across the 8 years of the study. Early winter months were not considered because low-quality records are concentrated during this period, as shown by the percentage of good-quality data obtained from MODIS metafile information (NASA LP DAAC 2013) (Fig. 1). Thus, we used this criterion to obtain a representative value for the spring productivity peak based on good-quality data. Per capita food availability was approximated by dividing both indicators of primary production (annual and spring) by population density.

Statistical analysis

In order to identify the factors driving inter-annual variation in recruitment, we fitted linear and generalized linear models to the young:female ratio, assuming a normal distribution of the error term. We used the identity link function as well as the logit and complementary loglog functions, recommended for proportion data (Crawley 2007). The independent variables considered were population density and both EVI-derived surrogates of primary productivity, annual EVI and spring EVI, considering the cycle previous to the birthing season. As the birthing season peaks in late spring, we expected that these measures express environmental conditions during gestation. These variables were tested independently (i.e., productivity indicators were not considered together in the same model). A second set of models included population density in the linear predictor, alone and linearly combined with annual and spring EVI. Finally, productivity indicators divided by population density, corresponding to measures of per capita food availability, were included as explanatory variables. Therefore we fitted eight models (seven models including a productivity indicator, population density or a combination of both, plus the null model that only included the intercept) to the data from each study location. Model selection was based on Akaike information criteria corrected for small sample sizes (AICc) (Burnham and Anderson 2002; Burnham et al. 2010). We first selected a set of models based on a delta AICc < 2 compared to the model having the lowest AICc. Among these candidates, we considered the most parsimonious model (i.e., fewer parameters). When candidate models had the same number of parameters, we chose the one with the lowest AICc. This procedure was used to analyze the data obtained at each location. In those cases where substantial non-linearity in the response variable was evident, we also fitted non-linear models. Here we present the results derived from a piecewise regression (Crawley 2007), which was the most parsimonious among various non-linear alternatives. We then used a maximum likelihood approach (Crawley 2007) to test if a single model could be used to represent the inter-annual variation in recruitment at both locations or if site-specific parameters were required. Model fitting was performed using the R software (version 2.15.2; the R Foundation for Statistical Computing, www.r-project.org). Piecewise regression break points were estimated using the package segmented for R.

Population projections

Finally, we used a deterministic model to test for the assumption that the studied populations were closed units, where reproduction and mortality alone could account

for the population growth observed at both locations. The alternative hypothesis was that population growth was aided by immigration from neighboring ranches. We constructed an age-structured population model and parameterized it with our recruitment data and maximal survival (0.99) for all age classes. Even though this maximal survival is an unrealistic assumption, it provides estimates of maximum potential population growth, making the rejection of our hypothesis conservative. For fecundity, we used the observed recruitment in each year of the recovery period when available, or predictions from our models based on the proxies of primary productivity selected (previous section) when recruitment data were not available (2007 at San Pablo; 2001–2005 at Cabo Dos Bahías). The model assumed a maximum age of 14 years (Amaya and von Thüngen 2001), first parturition at age 3 years and an even sex ratio at birth (Raedeke 1979). We projected the population from initial numbers at each location, keeping survival maximal and changing recruitment in every step according to our young:female data or model. Initial conditions at Cabo Dos Bahías were set in 2001, after the population crash in 2000, and at San Pablo in 2006, when the first population survey after sheep removal was conducted. Finally, we compared the projected population trajectory with the actual population trajectory based on density estimates in each location.

Results

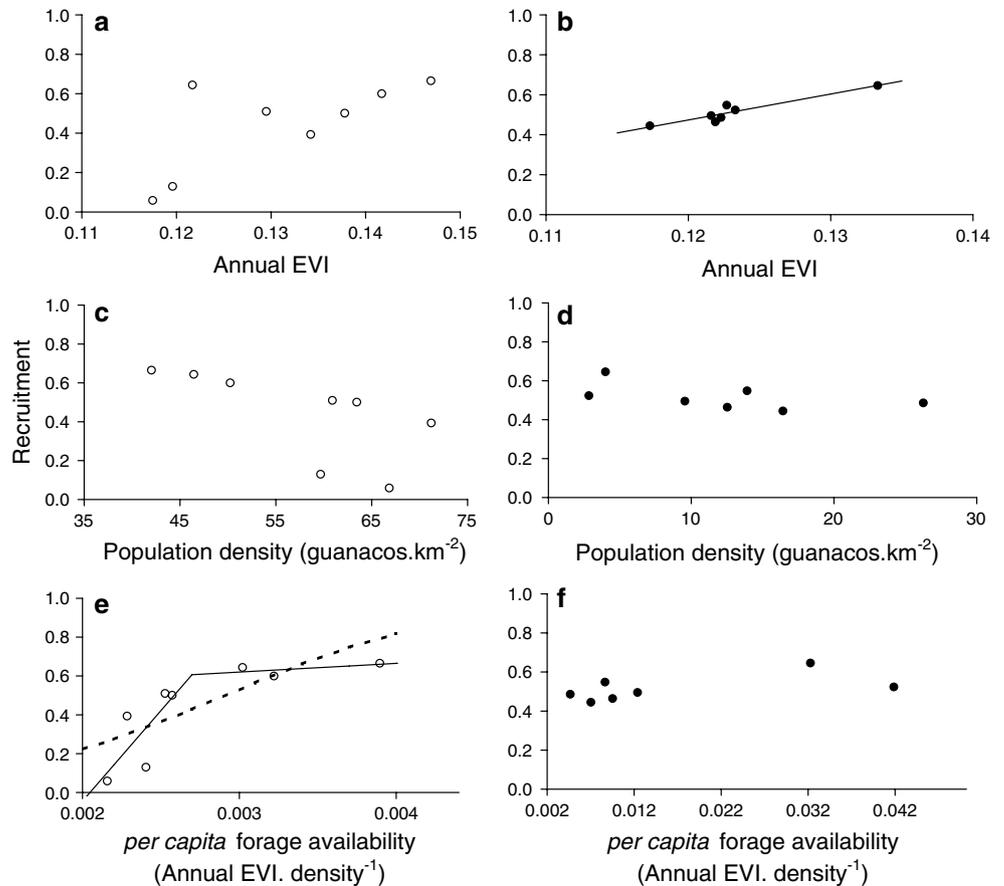
On average, annual primary production was higher at Cabo Dos Bahías than at San Pablo (Fig. 1) but this difference was only of 10 % (annual EVI difference = 0.013, SE = 0.004, $P = 0.0126$). Spring primary productivity was also 10 % higher at Cabo Dos Bahías but this difference was statistically non-significant (spring EVI difference = 0.014, SE = 0.008, $P = 0.088$).

Regarding recruitment, average values were similar between locations, although data for Cabo Dos Bahías were more variable than for San Pablo (Table 1), and relatively lower than those reported for other guanaco populations (Table 2). Model selection indicated that the factors driving inter-annual variation in recruitment also differed between locations. At San Pablo, recruitment was positively related to annual EVI (Fig. 2), whereas population density had no detectable effect. Model selection indicated that the identity link was the most parsimonious approach to describe this pattern given that the three links considered resulted in the same score (Table 3). In contrast, at the high-density Cabo Dos Bahías, variation in recruitment was explained by a combination of primary production and population density (Table 3, Fig. 2). We found a positive relationship between recruitment and both surrogates of per capita food

Table 2 Estimates of recruitment and reproductive rates in other locations, methods used and bibliographic sources

Location	Estimate	Parameter	Method	Reference
Tierra del Fuego	0.65	Pregnancy rate	Early uterine examination	Raedeke (1979)
Torres del Paine	0.70–0.75	Fecundity	Herd counts corrected by survival	Fritz and Franklin (1994) Sarno et al. (2003)
Peru	0.57	Fecundity	Visual assessment of pregnant females	Franklin (1975)
	0.34	Early recruitment	Herd counts	
Chubut	0.33–0.37	Early recruitment	Herd counts	De Lamo et al. (1982)

Fig. 2 Relationships between guanaco recruitment and variables of interest at Cabo Dos Bahías (a, c, e empty circles) and at San Pablo (b, d, f filled circles). Circles represent observed values of recruitment versus: a, b annual EVI; c, d population density; e, f proxy of per capita forage availability, expressed as annual EVI density⁻¹. Solid lines represent values predicted by final models, dotted line represents values predicted by the most parsimonious linear model (logit link function)



availability, annual EVI density⁻¹ and spring EVI density⁻¹. However, residual plots suggested that the logit function was not able to account for the lack of linearity and that a non-linear model would be more appropriate to describe this relationship. A piecewise regression on annual EVI density⁻¹ offered the best fit (Fig. 2e). A posteriori analysis of the entire data set (Cabo Dos Bahías and San Pablo data pooled) indicated that a piecewise model with a single asymptote performed better than a model with separate *n* [likelihood test, sum of squares = 0.041, *F* = 4.218, *P*(>*F*) = 0.067].

$$\text{Recruitment} = -1.5343 + 931.56 \times X \quad \text{if } X \leq X_c$$

$$\text{Recruitment} = 0.5542 + 0.0444 \times X \quad \text{if } X > X_c$$

$$X = \text{annual EVI} \times (\text{population density}^{-1})$$

$$X_c = 0.002239 \text{ annual EVI} \times (\text{population density}^{-1})$$

$$95\% \text{ CI}_{X_c} = 0.001989; 0.002489$$

Table 3 Differences in scores of Akaike information criteria corrected for small sample sizes between each model and the top-ranked model for recruitment within each location

GLMs	<i>k</i>	San Pablo			Cabo Dos Bahías		
		Linear	Logit	Comp loglog	Linear	Logit	Comp loglog
Intercept (<i>I</i>) ^a	1	10.9	10.9	10.9	3.45	3.45	3.45
<i>I</i> + Annual EVI	2	0.0	0.0	0.0	1.75	1.98	2.10
<i>I</i> + Spring EVI	2	12.8	12.8	12.8	5.25	5.20	5.12
<i>I</i> + Density	2	12.5	12.5	12.5	2.28	2.11	2.04
<i>I</i> + Annual EVI + Density	3	6.5	6.5	6.5	3.40	3.74	9.44
<i>I</i> + Spring EVI + Density	3	19.5	19.5	19.5	6.55	6.61	6.98
<i>I</i> + Annual EVI Density ⁻¹	2	11.9	11.9	11.9	0.10	0.00	1.00
<i>I</i> + Spring EVI Density ⁻¹	2	12.4	12.4	12.4	2.11	2.09	2.54

Annual and Spring EVIs as indicators of relative annual and spring primary productivity, respectively; annual and spring EVIs divided by population density are considered proxies of per capita forage availability. Linear, logit and complementary loglog refer to the link functions considered

GLM General linear model, *k* number of parameters in the model

^a Single-parameter model that includes only the intercept (*I*), and was considered the null model

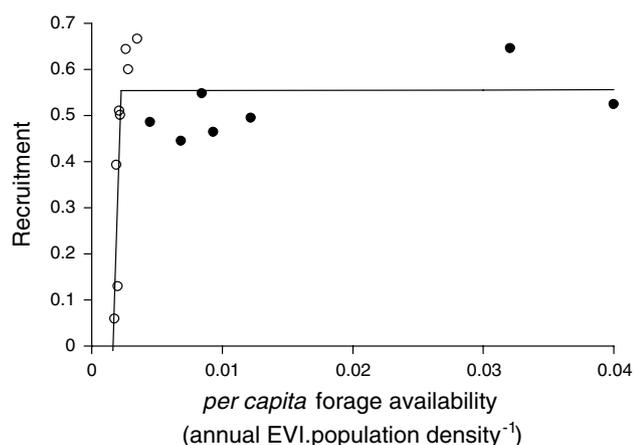


Fig. 3 Predicted values of recruitment as a function of per capita forage availability. Empty circles represent observed values at Cabo Dos Bahías, filled circles represent observed values at San Pablo. Forage availability is expressed as annual EVI density⁻¹

According to this overall, general model, recruitment stabilizes at 0.56 young per female, corresponding to per capita food availability of 2.239×10^{-3} EVI (guanaco km^{-2})⁻¹ (Fig. 3).

Finally, the comparison of the finite rate of increase of the theoretical projected populations with the actual densities showed that both populations grew much faster than expected under the assumption of no immigration (San Pablo $\lambda_{\text{projected}} = 1.172$, $\lambda_{\text{observed}} = 1.364$; Cabo Dos Bahías $\lambda_{\text{projected}} = 1.184$, $\lambda_{\text{observed}} = 1.362$) (Fig. 4). These results held even when observed densities were compared with a projected population assuming maximal possible recruitment for a guanaco population and null mortality ($\lambda = 1.266$).

Discussion

Average recruitment

The average recruitment at San Pablo and Cabo Dos Bahías are in agreement with other studies conducted in Chubut but are lower than reported for other locations such as Tierra del Fuego and Torres del Paine (Fritz and Franklin 1994; Raedeke 1979; Sarno et al. 2003). The young:female ratio is a composite measure resulting from various demographic processes, including fecundity rates and postnatal survival (Bonenfant et al. 2009). If environmentally driven factors such as mortality sources operating on newborns vary among locations, spatial differences in recruitment are expected. Where pumas are abundant, young guanacos can be preyed upon about four times as much as adults and high mortality can occur during the first months of life, as observed in Torres del Paine (Sarno et al. 1999). However, in our study locations there are no predators or hunters and main mortality sources are perimeter fences at San Pablo and winter starvation at Cabo Dos Bahías (A. Marino, unpublished data). Thus, we believe that inter-annual variation in our young:female ratio is reflecting reproductive variability and early juvenile mortality. In other ungulate species, females in poor body condition are less likely to breed (Mitchell and Brown 1974) or to produce a healthy offspring (Clutton-Brock et al. 1982). Between-population comparisons indicated that the quality and quantity of resources available for red deer (*Cervus elaphus*) females influenced their body condition and fecundity (Clutton-Brock et al. 1982). Therefore, in a less productive setting, a lower proportion of females would be capable of reproducing successfully. The lower recruitment observed

Fig. 4 Population density at **a** Cabo Dos Bahías and **b** San Pablo during the study period (circles point estimates, bars SEs); population density predicted by the observed recruitment under the assumption of closed populations (solid line); population density predicted by maximal recruitment possible for a guanaco population, under the assumption of closed populations (dotted line)

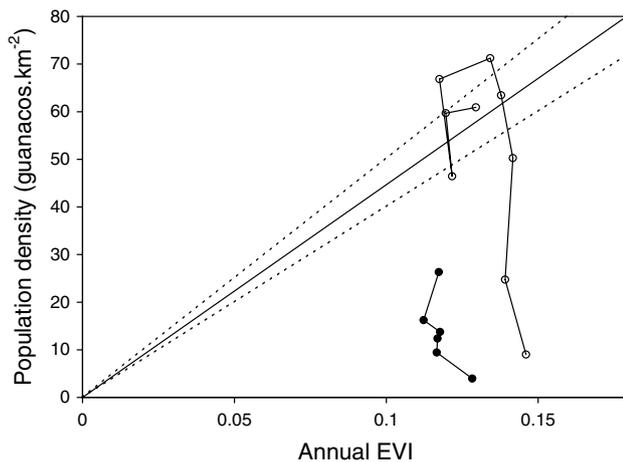
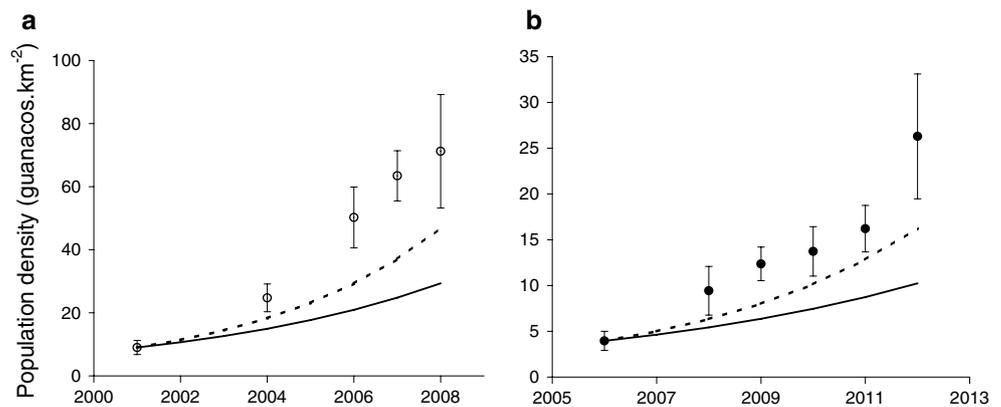


Fig. 5 Annual EVI and population density combinations that would define density-dependence threshold on recruitment (solid diagonal), and their corresponding 95 % confidence limits (dotted lines). Lower-right side of the figure represents the density-independent zone; upper-left side represents the conditions under which density dependence might operate on recruitment. Empty circles indicate the population trajectory for Cabo Dos Bahías (high-density setting); filled circles indicate the population trajectory for San Pablo

in this study when compared to values reported for more productive areas such as Tierra del Fuego and Torres del Paine, may be related to differences in rainfall regimes and the consequent lower primary productivity of our study locations.

Ecological drivers of guanaco recruitment

Although average values were similar, recruitment correlates differed between San Pablo and Cabo Dos Bahías. In the low- to medium-density San Pablo, only forage availability seemed to have an effect on recruitment, whereas forage availability and density affected recruitment at Cabo Dos Bahías. Thus, annual primary production was a major factor driving variation in recruitment at both locations. This result suggests that environmental carrying capacity

can strongly vary from one year to the next. This hypothesis was supported by a long-term study on a vicuña population (*Vicugna vicugna*) of northern Chile, the other camelid species of South America. Shaw et al. (2012) showed that a logistic model with a fluctuating, rainfall-dependent carrying capacity fits vicuña census data better than a simple logistic model. Variable carrying capacity may have crucial implications for wildlife management. For example, rainfall variability precluded a stable estimate of the maximum sustainable yield in order to prescribe harvest quotas of several species of kangaroos by the Australian government (Pople and Grigg 1999), stressing the role of environmental stochasticity in shaping herbivore dynamics.

In addition to the effect of annual primary production, in the high-density scenario (Cabo Dos Bahías), recruitment showed a negative relationship with population density. This result indicates that variable primary productivity and density dependence operate jointly in the high-density setting. Therefore, recruitment may be reduced either by increasing population density or by decreased productivity, through the combined variable per capita forage availability. Both factors seem to interact to affect recruitment, amplifying density dependence in poorer years, as suggested by Bonenfant et al. (2009). Empirical evidence of density dependence in a guanaco population was documented in Torres del Paine, Chile, where birth mass was inversely related to population density (Sarno and Franklin 1999). Raedeke (1979) found evidence of density dependence on adult and juvenile survival from guanacos in Tierra del Fuego, but young:female ratios did not vary with population density. However, marked differences in methodologies, primary productivity, climate, predation and hunting pressure among studies prevent drawing conclusions from comparisons with our results. Concerning other ungulate species living in fluctuating environments, McCullough (1999) pointed out that pronounced short-term declines in carrying capacity due to high environmental variability may have an important effect on population dynamics and even undercut intermediate-size populations periodically.

Other studies have shown that the notion of per capita food availability is essential to understand the changes in carrying capacity and the factors regulating population growth (Pierce et al. 2012; Sinclair et al. 1985). In accordance with these ideas, our findings indicate that including environmental variability is crucial to model ungulate population dynamics and suggest that overlooking temporal changes in carrying capacity may lead to erroneous conclusions. In highly variable systems, the unaccounted for variability in carrying capacity may even mask density dependence as well as other important processes, as a result of a failure to assess actual per capita resource availability.

Regarding the density-dependence function, the logistic equation widely used to represent population growth assumes a linear decline in population growth with increasing n . However, empirical evidence indicates that density-dependence responses of demographic rates are most often non-linear, being strongest at high density than at low density (Fowler 1987). This pattern was reported for mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), among other ungulates living in moderately productive environments (McCullough 1999). Such a response indicates that populations grow at a relative constant rate over low and medium population sizes, with density effects occurring near carrying capacity (McCullough 1999). Therefore, a threshold in population density over which density dependence operates can be inferred. Our recruitment results are in accordance with this idea, with no density effects in the low- to medium-density setting and a strong density effect, combined with carrying-capacity variation in the high-density scenario. Because in our system per capita food availability is determined by both annual primary production and population density, the threshold estimated by our model indicates a range of primary productivity and population density combinations below which the effect of food limitation on recruitment might become evident. This breakpoint can be interpreted as the slope of a linear relationship between primary productivity and population density separating density-dependent from density-independent zones through all possible combinations of these variables (Fig. 5). The higher the breakpoint, the steeper the relationship and a faster population regulation can be expected.

Recruitment patterns seem to be consistent between Cabo Dos Bahías and San Pablo, and our results, although preliminary due to the small sample size and the limited range of comparable density conditions, suggest that a single model could represent recruitment variation at both locations. However, extrapolation from these conditions would be unsafe because specific environmental conditions such as environment heterogeneity, quality of food resources, scale of landscape over which populations occur, as well as the associated dispersal capability, can reshape the density-dependence function (McCullough 1999).

Dispersal capacity may have a strong effect on density-dependence functions at Cabo Dos Bahías provided that its potential dispersal perimeter is reduced due to geomorphological features (i.e., cape: headland extended into a body of water). Therefore, our specific model might fail to represent adequately guanaco dynamics at other locations where an increased dispersal rate may buffer the intensity of density dependence on recruitment. Hopefully, future studies on the still-increasing population at San Pablo will help to test the accuracy of our general model to represent guanaco recruitment variation in a novel high-density setting.

Several studies have indicated that there are important differences in the strength of density dependence between ages, sexes, among cohorts and even between individuals of the same cohort, and that such variation can generate complex population dynamics (Bonenfant et al. 2009). In particular, our recruitment estimates could be deflated given the potential of a high proportion of sub-adults entering the population through immigration, thus confounding our results. Unfortunately, we lack the detailed data on age structure required to assess these effects in our study sites. However, both populations experienced strong immigration but only the high-density Cabo Dos Bahías population showed deflated recruitment. Therefore, we can infer that the most likely factor driving recruitment decrease was food limitation. We have found clear recruitment correlates, suggesting that the effect of food availability is strong enough to become evident, regardless of all potential confounding factors and reduced sample sizes. Still, given the high spatiotemporal variability inherent to arid systems, longer time series and additional locations are needed in order to confirm these findings and better understand the processes affecting guanaco demography.

Closed populations assumption and management implications

Both studied populations grew at higher rates than our theoretical projections based on maximal possible growth for closed guanaco populations. Recruitment alone was not high enough to generate the observed recovery and, therefore, strong immigration must have taken place during the study period in order to make the observed growth rate possible. Consequently, we rejected the assumption that the studied populations were closed units. As we lack mortality data at this time, we cannot elaborate on the relative importance of recruitment and immigration as influencing population growth rates. Our results, however, highlight the misconception of assuming a guanaco population as a closed unit when fences are those typical of Patagonian sheep ranches (i.e., 1-m-high wire fences). Such fences may cause fatalities but, clearly, do not prevent guanaco

movements. Previous studies have documented massive movements of guanacos between ranches as short-term responses to management changes (Baldi et al. 2001; Sarno et al. 1999). Dispersal can be a dominant regulating agent through population expansion or colonization of empty areas (Bonenfant et al. 2009) and failure to account for spatial patterns in population dynamics may lead to incorrect conclusions (Jonzén et al. 2005). Hence, our results suggest that in order to accurately assess the value of alternative management actions, resource administrators should avoid closed-population assumptions when working at a small spatial scale (i.e., ranch or group of small ranches). Moreover, accounting for guanaco dispersal among management units, particularly massive movements triggered by radical changes in guanaco and/or live-stock loads, seems to be essential to adequately represent guanaco dynamics.

To our knowledge, these are the first estimates of guanaco recruitment and its links with inter-annual changes in density and forage availability, without the confounding effects of predation, inter-specific competition or hunting. The analyses of the ecological correlates of vital rates variation and the use of conceptual models that emphasize basic processes and assumptions, previously recommended by several authors (Coulson et al. 2000; Gaillard et al. 1998; McCullough 1999), have allowed us to address relevant aspects of guanaco demography. Among them, carrying-capacity variability and its interaction with density dependence, as well as the open nature of guanaco populations within ranches, have important theoretical and applied implications.

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