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Factors influencing guanaco distribution in southern Argentine Patagonia and implications for its sustainable use

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Abstract The Guanaco (*Lama guanicoe*) has suffered a progressive decline in numbers because of unregulated hunting and poaching by an assumed competition with sheep. Inadequate livestock management, including keeping sheep numbers above carrying capacity, has led to a degradation of the Patagonian steppe. Recently, interest has grown towards a reduction in sheep density and diversification of extractive activities. Guanaco populations could be potentially amenable to a number of sustainable uses. Our aim was to investigate the factors that determine guanaco distribution in southern Argentine Patagonia and to generate a predictive cartography at the regional scale. We hypothesized that guanaco distribution could be determined by primary productivity, terrain ruggedness, human disturbance and poaching, and competition with livestock. Guanaco surveys were performed from vehicles using a road survey method. To analyze the relationship between guanaco occurrence and potential predictors we built Generalized Additive Models (GAMs) using a binomial error and a logistic link. We found that guanaco occurrence increased in the less productive and remote areas, far from cities and oil camps, and decreased in regions with high sheep density. These results suggest that guanacos tend to occur where human pressure is lower. One way to promote guanaco conservation would be to highlight the economic value of guanacos under the regulations imposed by a sustainable exploitation of their populations. The predictive models developed here could be a useful tool for the implementation of conservation and management programs at the regional scale.

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Introduction

The guanaco, *Lama guanicoe*, the largest wild terrestrial herbivore in South America, is distributed in a wide range of arid and semi-arid habitats, from sea level to 4,500 m on the Andes, from northern Peru to central Chile, and across the Argentinean and Chilean Patagonia. In spite of being considered a highly adaptable camelid with a wide distribution and flexibility in its use of resources (Franklin 1983; Puig 1995), the guanaco has suffered a progressive decline in numbers and a parallel reduction of its geographic range (Franklin et al. 1997). The historical distribution of the guanaco has been reduced by 75% in Chile and Peru and 60% in Argentina (Franklin et al. 1997). Currently more than 90% of guanaco populations occur in Argentina, of which 70% live in the Patagonia (Puig 1995), mostly in Santa Cruz (Baldi et al. 2006), the southernmost and largest continental province.

This decline has been attributed to unregulated hunting and poaching (Franklin 1983; Cunazza et al. 1995; Puig 1995; Donadio and Burskik 2006) prompted by an assumed competition with sheep for water and food (Franklin 1983; Baldi et al. 2001, 2004). Although the guanaco is not considered a threatened species at the continental level, some populations could be at risk of disappearing (Cunazza et al. 1995). In addition, most populations are restricted to areas with low primary productivity (Franklin et al. 1997; Travaini et al. 2007).

In Santa Cruz, inadequate livestock management, including keeping sheep numbers above carrying capacity (Golluscio et al. 1998) and overgrazing of mesic sites (Mazzoni and Vázquez 2004) has lead to steppe degradation and, in a positive feedback, to a further decrease in carrying capacity of pastures for sheep. As a consequence many ranches were deserted. Acknowledging this as the probable mechanism causing the failure of sheep production, interest has grown towards reduction in sheep density and diversification of extractive activities in the Patagonian shrub-steppe (Puig 1992; Franklin et al. 1997; Baldi et al. 2006; Travaini et al. 2007). Guanaco populations could be potentially amenable to a number of sustainable uses, including production of meat (Soto et al. 1991), leather (Ojeda and Mares 1982), wool (Sacchero et al. 2006), as well as a valuable element for wildlife tourism (Franklin et al. 1997; Anonymous 2002).

Confirming or discarding proposed agents of guanaco decline, or identifying new ones, is required to prevent further contraction of its geographic range as well as to promote diversification of land uses across the Patagonian steppe. Agents of decline have been traditionally drawn from local studies in small protected areas (Baldi et al. 1997; Sosa and Sarasola 2006; Puig et al. 2008). However, large-scale studies are necessary to detect patterns of distribution (Scott et al. 2002) and to link them with regional processes involved in guanaco decline. Moreover, determining distribution patterns is crucial to highlight areas where sustainable exploitation of guanaco populations could be an option for use diversification.

The aim of this study was to investigate the factors that determine the distribution of guanaco populations in the southern Argentine Patagonia and to generate a predictive cartography of guanaco distribution at the regional scale. We hypothesized that guanaco distribution is determined by several factors that could act concurrently: primary productivity, terrain ruggedness, disturbance and poaching, and competition for food with livestock. Specifically, the respective predictions of these hypotheses were that the probability of finding guanacos would be higher: (1) in more productive environments and close to wetlands, since they offer more abundant forage of better quality; (2) in flat open areas, where vigilance and quick escape are facilitated; (3) away from cities and oil camps, because of the higher accessibility and hunting pressure close to these areas; and (4) in areas with low levels of sheep ranching activity, because of potential competition with sheep for forage and active persecution by ranchers.

Methods

Study area

Santa Cruz (46°–53° S; 65°–73° W) has an area of 245,865 km^2 (6.5% of Argentina; González and Rial 2004). The relief features hills and plains whose vegetal cover is dominated by a mixed steppe of grass and shrubs, rarely exceeding 0.5 m in height (Movía et al. 1987). *Nothophagus* forest occurs in the Andean slopes, whereas lowlands are dominated by shrub-steppe. The climate is dry and cold with strong westerly winds, and varies along a marked gradient, with precipitation decreasing from west to east, and temperature from northeast to southwest (González and Rial 2004).

Sampling unit selection

Before conducting field studies, we established which tracks (road segments) would be surveyed. For the selection of the sampling units, we stratified the study area into twelve regions (or strata) based on a combination of mean NDVI (Normalized Difference Vegetation Index, a measure of primary productivity) and mean slope, because vegetation productivity could be an important driver of guanaco distribution, and mean slope since detection could be affected by terrain irregularity.

Using vector data of road coverage we randomly selected road segments that added up to 4,500 km for the first austral spring-summer. To guarantee that every strata was properly sampled, 1,500 km were equally distributed among survey strata (125 km on each stratum) and 3,000 km were distributed proportionally to the area of each stratum. During the second spring-summer, we survey 3,500 km of new road segments, which means that about 90% of available national and provincial roads in Santa Cruz were surveyed.

Field survey

Field-work was conducted during two consecutive austral spring-summers (November 2004–February 2005 and December 2005–January 2006). Surveys were performed by two observers from a vehicle driven at a maximum speed of 40 km/h. We selected this methodology because of the open nature of the steppe environment, the low density of wildlife, and because it allows more area to be covered in a fixed amount of time compared with other methods (Travaini et al. 2007).

For each sighting, we stopped the vehicle and recorded group size and identified the social unit. During the breeding season, guanacos are grouped into three types of social units (Franklin 1983; Ortega and Franklin 1995): family groups, made of one territorial male and several females with their offspring; male groups, formed by non-breeding, mainly young individuals; and solitary males that seek or defend a territory without females. Since both sexes are morphologically indistinguishable in the field (Franklin 1983), family groups were distinguished from male groups by the characteristic defensive behavior of the adult male, which tends to stay apart from other individuals, adopting a dominant position, while females and juveniles form a compact group, and by the presence of distinctly small juveniles (Puig and Videla 1995; Marino and Baldi 2008). Males form big loose groups (Ortega and Franklin 1995; Puig and Videla 1995) and solitary individuals are assumed to be males only (Ortega and Franklin 1995).

We measured the distance to the animal or to the center of the group with a laser range finder (Leica LRF 1200 Rangemaster), as well as the angle of the animal relative to our bearing. We obtained our bearing relative to north from the inertial compass in the GPS unit (Garmin GPS MAP 76CS). Guanaco sightings were collected in a PDA (Personal Digital Assistant; PDA Tungsten T3) synchronized with the GPS, which was used to record the trajectory and location of the survey track, as well as the date, time, and actual speed for each observation. Distance and angle in relation to North allowed us to obtain the actual positions of guanacos. During the survey, we also recorded the number of sheep observed for modelling sheep occurrence, because official statistics on distribution and number of sheep were not available.

Environmental predictors

We selected ten potential environmental predictors that summarized the most relevant environmental gradients and landscapes features needed to test our four hypotheses about the factors influencing the regional distribution of guanacos (Table 1).

Table 1 Predictions derived from four hypotheses about the factors influencing guanaco distribution, and variables used as predictors in models testing them

Description hypothesis	Variables
Forage hypothesis guanaco are associated with the most productive environments because they offer better quality forage	*Mean_NDVI*: mean normalized difference vegetation index *Growth_period*: length of the vegetation growth period defined as the mean number of 10 day periods with NDVI values > 85 *CV_NDVI*: coefficient of variation of NDVI *Season_MAX*: month at which the NDVI reaches its annual maximum value *Distance_wetland*: distance to the nearest successional pond-bog-wet meadow
Topography hypothesis guanaco are associated with flat open areas where antipredator vigilance and quick escape are facilitated	*Altitude*: mean altitude in m.a.s.l. in a 1-km pixel *Slope*: mean slope in degrees in a 1-km pixel
Poaching hypothesis guanaco avoid cities and oil camps as a consequence of greater hunting pressure close to these areas	*Distance_urban*: distance to the nearest city *Distance_oil*: distance to the nearest oil camp
Sheep ranching hypothesis guanaco avoid areas of intensive sheep ranching because of potential competition with sheep for forage and active persecution by ranchers	*Density_sheep*: relative probability of contact with a sheep flock in vehicle surveys calculated per ranch

We derived vegetation productivity variables from the VEGETATION sensor on board of SPOT-4 satellites (http://www.spot-vegetation.com) that monitor daily terrestrial vegetation cover at 1-km spatial resolution. We used NDVI images to estimate primary productivity (mean NDVI and its coefficient of variation), month at which the NDVI reaches its annual maximum, and seasonality in vegetation growth using seven consecutive years of data (April 1999–March 2005). We acquired topographic data from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov/srtm). We estimated the mean slope and altitude at 1-km cells using SRTM data with a resolution of 90 m. Distances from each cell to the nearest city or oil camp were calculated from IGM (2005), and distance to the nearest meadow from Mazzoni and Vázquez (2004). The probability of sheep occurrence was taken from a predictive map built with data recorded during our surveys (authors unpub. data).

Multicollinearity could make comparison of alternative models difficult (Lennon 1999). We considered two predictors to be collinear when Spearman rank correlation coefficients were >0.7. Among strongly correlated predictors, we retained those with the clearest ecological meaning for the species (Austin 2007).

Effective area surveyed and detectability

Tracks recorded with GPS units defined the actual trajectory of our survey. We used the distances to individual guanacos or groups to estimate the area effectively covered by the survey. We used the Hazard-Rate key with two parameters and cosine adjustment term model in DISTANCE 5.0 software (Buckland et al. 2001) to fit a detection function to the distance data. A 400-m buffer on both sides of the track was chosen to define the effective area surveyed since the 75% of all guanaco sightings fell within this effective area.

Presence/absence modeling requires defining units in which presence or absence is recorded. In this case we used 1-km grid cells, given by the spatial resolution of NDVI data. We overlaid the surveyed tracks with 400-m buffers on top of this 1-km grid and selected all grid cells that partially or totally overlapped with buffers. Guanaco sightings ($n = 992$) were overlaid with selected cells. Grid cells with ≥ 1 sighting were considered presences and the remaining cells were considered absences.

The probability of detecting a solitary individual or a group in a 1-km cell was affected by the proportion of the cell that was effectively surveyed. We calculated the variable "Area_surveyed" as the fraction of the cell surface included in the 400-m buffer at both sides of the survey transect. This variable was included as a fixed term in the models using a spline with 3 df to correct for its effect on the detection probability (Travaini et al. 2007). Other survey specific variables could also influence guanaco detectability, such as car speed (Speed), time of day (Time_day), or calendar date (Date). We tested the effect of these variables on guanaco detectability, and significant variables were included as correction terms in the models.

Model fitting

We fitted generalized additive models (GAMs, Hastie and Tibshirani 1990) to the presence/absence of guanaco using a binomial error and a logistic link. Due to the quite different number of presences ($n = 685$) and absences ($n = 13{,}739$), we decided to use a resampling scheme (McPherson et al. 2004; Liu et al. 2005). We randomly chose 548 out of the 13,739 empty cells (i.e. a number equal to 80% of presence cells) to build a model together with 548 randomly chosen cells with guanaco presence. We repeated this procedure 100 times. Predictors were selected from the initial set by a backward–forward stepwise procedure, starting from a full model that included all potential predictors relevant to a particular case, by using the *step.gam* routine in S-PLUS 2000 (MathSoft 1999). Predictors were included initially in the models as smoothing splines with 3 df. The Akaike's Information Criterion (AIC) was used to retain a term or to simplify it by reducing the df of the spline (Sakamoto et al. 1986).

To compare alternative models within a hypothesis that were as good as the best model in terms of AIC (Burnham and Anderson 2002) we fitted the models to a single matrix with the complete data-set where original prevalence was maintained (Jiménez-Valverde and Lobo 2006). We considered as competing models those whose Δ AIC value was <4.0. Finally, we built a general model with all relevant variables retained in the most parsimonious model representing each of the hypotheses.

Model validation

Each time a data-set was generated to build a model the remaining 20% of the original data was used to validate it. Models were parameterized and tested 100 times with random samples of an equal number of presences and absences that had not been used to fit the model. The area-under-the-curve (AUC) of the receiver operating characteristic (ROC) plot was computed for each of the 100 models to assess the predictive power of the logistic models (Murtaugh 1996). The AUC varies from 0, when model discrimination is not better than random, to 1, when the model has a perfect discriminatory ability (Pearce and Ferrier 2000). Predictive models should have an AUC $\geq$ 0.7 to be considered useful (Harrell 2001). Differences between the mean predictive ability of each model and the mean predictive ability of the best model were tested with a Wilcoxon–Mann-Whitney test (Crawley 2002).

Generating a predictive cartography of guanaco distribution

We used the most parsimonious model to build a predictive cartography of guanaco occurrence. To produce this cartography, we used the option in IDRISI Kilimanjaro (Eastman 2003) to export predictors as a data matrix to S-Plus, applied the *predict.gam* procedure to make predictions based on the new data matrix, and then exported the predicted probability values at the scale of the response from S-Plus back to IDRISI to produce a probability map.

Results

The variable Area_surveyed had a significant effect in all binomial models. As expected, the probability of observing guanacos in a 1-km^2 cell increased significantly with the proportion of the cell that was effectively surveyed.

The most parsimonious model of guanaco occurrence among those testing the forage hypothesis included Mean_NDVI, CV_NDVI and Distance_wetland (model 1; Table 2).Contrary to our prediction, we found that the probability of guanaco occurrence increased with distance to the nearest meadow, and decreased with increasing mean productivity and with increasing NDVI variability (Fig. 1a).

Only Slope was retained in the best model among those testing the topography hypothesis (model 4; Table 2). The probability of guanaco occurrence increased with

Table 2 Competing models of guanaco occurrence representing four hypotheses

Model code	Models	AIC	Δ AIC
	Forage hypothesis		
1	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wetland + CV\_NDVI$	3504	0
2	$Area\_surveyed_2 + Mean\_NDVI_3 + Distance\_wetland + CV\_NDVI$	3505	1.09
3	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wetland$	3508	4.01
	Topography hypothesis		
4	$Area\_surveyed_3 + Slope_3$	3584	0
5	$Area\_surveyed_2 + Slope_3$	3585	0.82
6	$Area\_surveyed_2 + Slope_3 + Altitude$	3587	2.77
	Poaching hypothesis		
7	$Area\_surveyed_3 + Distance\_urban_3$	3473	0
8	$Area\_surveyed_3 + Distance\_urban_3 + Distance\_oil_2$	3473	0.09
9	$Area\_surveyed_2 + Distance\_urban_3$	3474	0.74
10	$Area\_surveyed_2 + Distance\_urban_3 + Distance\_oil_2$	3474	0.84
11	$Area\_surveyed_3 + Distance\_urban_3 + Distance\_oil$	3474	1.34
12	$Area\_surveyed_2 + Distance\_urban_3 + Distance\_oil$	3475	2.13
	Sheep ranching hypothesis		
13	$Area\_surveyed_3 + Density\_sheep_2$	3561	0
14	$Area\_surveyed_2 + Density\_sheep_3$	3562	1.18
	General models		
15	$Area\_surveyed_2 + Mean\_NDVI + Distance\_urban_3 + Density\_sheep_3 + Distance\_wetland_2 + Altitude_2 + Speed + Date$	3170	0
16	$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_urban_3 + Density\_sheep_3 + Distance\_wetland_3 + Altitude_2 + Speed + Date$	3172	2.01

For each model, Akaike's Information Criterion (AIC) and the difference between AIC of the current model and the most parsimonious model (Δ AIC) are given. *Numeric subscripts* denote the df of the spline

Table 3 Assessment of the predictive power of best logistic models representing different hypotheses about the factors determining guanaco occurrence

Model	AUC ± SE	%
Poaching hypothesis	0.73 ± 0.03	88
Sheep ranching hypothesis	0.72 ± 0.03	77
Poaching + sheep ranching	0.75 ± 0.02	100

Mean AUC values are computed for 100 replicate parameterizations of the models. The percentage of models whose AUC was ≥0.7 is shown

slope, although this trend was not observed at high slope values (Fig. 1b). Hence, our hypothesis was not clearly supported.

The best model obtained among those testing the poaching hypothesis included only the variable Distance_urban (model 7; Table 2). The probability of guanaco occurrence strongly increased with the distance to the nearest city (Fig. 1c). However, four of six competing models also included the variable Distance_oil (models 8, 10–12; Table 2), indicating that guanaco occurrence increased with the distance to oil camps.

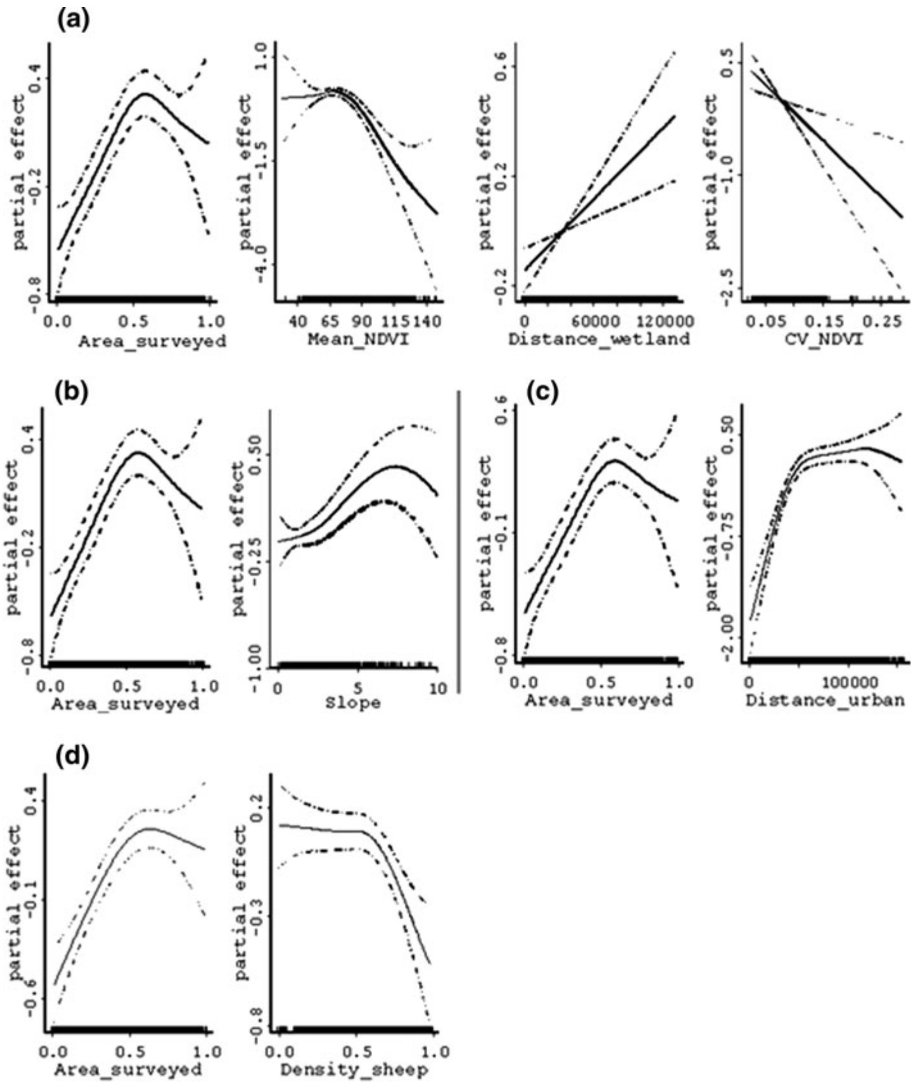

Fig. 1 Partial effects of predictors included in best models testing different hypotheses about the determinants of guanaco distribution (see model code on Table 2). **a** Forage hypothesis (model 1); **b** topography hypothesis (model 4); **c** poaching hypothesis (model 7); and **d** sheep ranching hypothesis (model 13)

The best model among those testing the sheep ranching hypothesis showed that the probability of guanaco occurrence was constant when sheep abundance took low to moderate values (<0.6) (model 13; Table 2; Fig. 1d). However, the probability of guanaco occurrence decreased in places with moderate to high values of sheep abundance (>0.6; Fig. 1d).

We compared the best models for the hypotheses that were supported by data and found that the models testing the poaching hypothesis had the lowest AIC value, followed by models testing the sheep ranching hypothesis (Table 2).

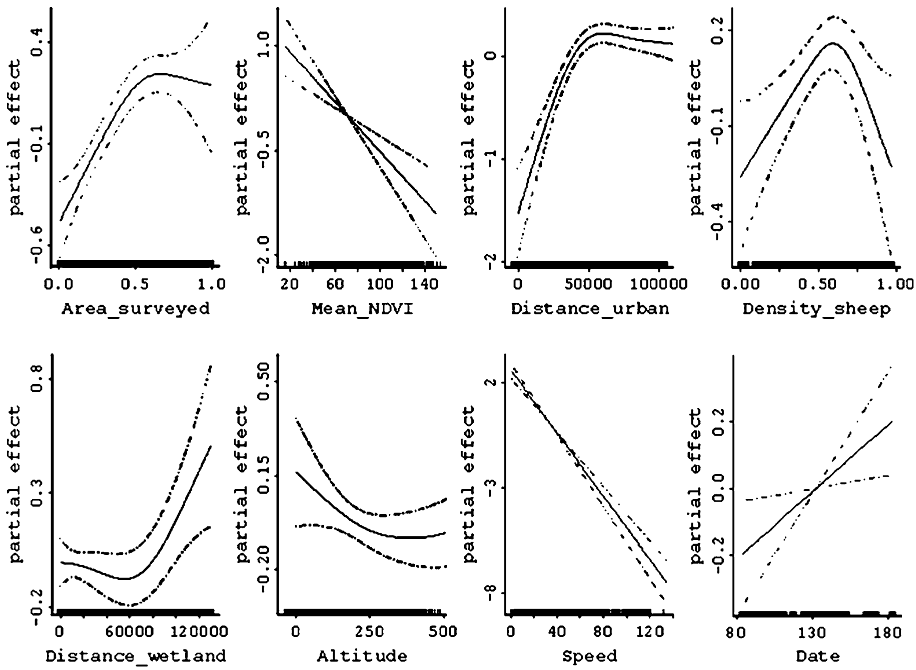

Fig. 2 Partial effects of predictors included in the best general model of guanaco distribution (model 15 in Table 2)

Most models were improved with the inclusion of the survey specific variables (Appendix), without altering the identity of predictors or the relative strength of their effects. We found a significant linear effect of Speed and Date on guanaco detection. The probability of detecting an individual increased with date and decreased with car speed. Among the general models tested, the most parsimonious one included Mean_NDVI, Distance_wetland, Distance_urban, Density_sheep, Altitude, Area_surveyed, Date and Speed (model 15; Table 2; Fig. 2).

Model validation

We obtained predictive models that performed better than a null model for every set of predictors (Table 3). Predictive models fitted the data well, with a mean (±SE) validation AUC ranging from 0.72 ± 0.03 to 0.75 ± 0.02, which suggests that selected models were robust and could be considered potentially useful for predicting the distribution of guanaco within the ranges of predictor variables (Edith 2000; Harrell 2001). Among general models, model 15 (Table 2) had the highest predictive ability, which was significantly higher than the predictive ability of best models representing the poaching ($Z = 5.22$, $P < 0.001$) and the sheep ranching hypotheses ($Z = 8.59$, $P < 0.001$).

Predictive cartography of guanaco distribution

Predictions of model 15 (Table 2) were translated to a GIS assuming that whole 1-km cells were effectively surveyed at 30 km/h at the most favorable date in the middle of

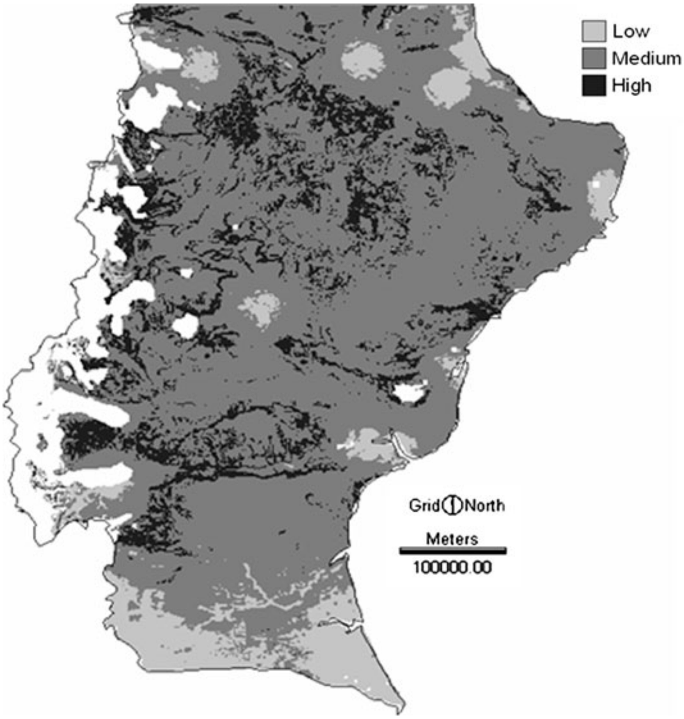

Fig. 3 Probability of guanaco occurrence in Santa Cruz province, Argentina. Probabilities obtained from model 15 (Table 2) were categorized into three classes (low: <0.33, medium: 0.33–0.66, high: >0.66) for ease of interpretation. Areas in *white* correspond to regions without predictions: sea, lakes, forested areas, or outside the model's environmental space

spring-summer period (i.e. January 13). Thus, the probability map shown in Fig. 3 takes into account all the effects contained in this model. To facilitate visualization, we simplified the relative probability of occurrence into three classes (Fig. 3). Areas with a high probability of guanaco occurrence were more abundant toward the center of the study area, while lower probabilities were mainly restricted to the south. Additionally, areas of low probability around urban areas were scattered across the entire region.

Discussion

Contrary to the predictions of the forage hypothesis, we found a negative relationship between guanaco occurrence and primary productivity, and a positive one with the distance to the nearest wetland. These relationships suggest that guanacos are more often found in less productive areas. Our results also suggest that the probability of guanaco occurrence is higher in high ground and rugged areas, contrary to the predictions of the topography hypothesis. It seems unlikely that use of less productive areas and rugged terrain would provide any advantage, compared with flat productive meadows. Puma (*Puma concolor*), the only natural predator of guanacos, employs an ambush hunting strategy that should be more efficient on rugged terrain with woody vegetation than in open grassy meadows (Wilson 1984; Bank and Franklin 1998; Sarno et al. 1999). As pumas do not chase their prey across long distances, guanacos could reduce predation risk by selecting open flat habitats, because an early detection could enhance the opportunities to escape (Bank et al. 2002). Moreover, guanaco vigilance has been reported to be higher in rugged habitats than in flat ones (Marino and Baldi 2008). Therefore, guanaco association with rugged, less productive terrain may not reflect true habitat preferences but an indirect response to a third factor.

We found a positive association of guanaco with remote areas, far away from centers of human influence such as cities and oil camps. Areas of low probability of guanaco occurrence were clearly associated with urban areas. These results suggest that human activity has a direct and negative effect on guanaco occurrence, probably indicating either a behavioral avoidance of sites where predation risk by humans is high and recurrent, or a true decline of guanaco local population due to overhunting. Donadio and Burskik (2006) report that hunting harassment of guanacos affects the balance between energy intake and expenditure, and also induces changes in habitat preferences, so that animals may select less productive but more secure areas. Intensive harassment by hunting could produce a negative impact on survival by forcing individuals to make a disproportionate use of their energetic reserves (Cajal 1991). Consistently with our interpretation, in the absence of hunting guanacos prefer areas with high primary productivity and abundant rich forage, preferably in plain terrain (Bank et al. 2003; Puig et al. 2008).

The occurrence of guanaco decreased as the probability of sheep occurrence increased, in agreement with the results of others studies reporting a negative relationship between the abundances of guanaco and sheep. This pattern has been interpreted as a result of direct competition for forage, without discarding the possibility of active guanaco persecution by humans (Puig et al. 1997; Baldi et al. 2001). While these studies were carried out at the local scale, our probability map shows that the same pattern holds at the regional scale. Areas with low probability of guanaco occurrence are concentrated in the south of Santa Cruz, where productive habitats abound (González and Rial 2004). Southern regions are mainly devoted to extensive sheep ranching. Historically, guanaco and upland goose (*Chloephaga picta*) were considered pests by ranchers on the basis of an assumed competition with sheep for water and food (Baldi et al. 2001, 2004; Blanco and De la Balze 2006). On the contrary, areas of medium to high probability of guanaco occurrence clumped around the center of Santa Cruz. These areas correspond with the so called 'central high plateau', a region containing the least productive steppe in the whole region, where severe steppe degradation affects 77% of the land (Borrelli et al. 2004). Unsustainable use of rangelands has been followed by progressive land abandonment in over 60% of Santa Cruz. Consequently, the medium–high probability of guanaco occurrence in this region might be due to low human disturbance, as an indirect effect of steppe degradation and subsequent abandonment, as well as poor accessibility.

Since sheep ranching is the prevalent land use and a major economic driver in southern Patagonia, the conflict between sheep and guanacos is an important threat to guanaco conservation. The poaching and sheep ranching hypotheses were supported by our data, suggesting the prevalence of human over environmental or natural factors as determinants of guanaco distribution at the regional scale. Guanacos seem to occur where human pressure is released as it happens with many species subjected to persecution (Caughley and Gunn 1996). This implies that reducing disturbance and hunting pressure, and turning farmer's attitudes more favourable towards guanaco may potentially halt guanaco decreasing population trends throughout most of Patagonia. Therefore, one way to promote guanaco conservation would be highlighting the economic value of guanacos under the regulations imposed by a sustainable exploitation of their populations. The predictive models created in this work could be a useful tool for the implementation of such conservation and management programs at the regional scale. The map we provide represents the present guanaco distribution under human disturbance and hunting pressure. Care should be taken as the areas where the probability of guanaco occurrence is higher do not necessarily represent better habitats for the species.

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Appendix

See Table 4

Table 4 Competing models of guanaco occurrence after correcting for survey specific factors

Models	AIC	Δ AIC
Forage hypothesis		
$Area\_surveyed_3 + Mean\_NDVI_3 + Distance\_wetland + CV\_NDVI + Speed_3 + Date_3 + Time\_day_3$	3244	0
$Area\_surveyed_3 + Mean\_NDVI_3 + CV\_NDVI + Speed_3 + Date_3 + Time\_day_3$	3246	1.39
$Area\_surveyed_3 + Mean\_NDVI_3 + CV\_NDVI_3 + Speed_3 + Date_3 + Time\_day_3$	3247	2.62
$Area\_surveyed_3 + Mean\_NDVI_2 + CV\_NDVI + Speed_3 + Date_3 + Time\_day_3$	3248	3.92
Topography hypothesis		
$Area\_surveyed_3 + Slope_3 + Altitude + Speed_3 + Date_3 + Time\_day_3$	3312	0
$Area\_surveyed_3 + Slope_3 + Speed_3 + Date_3 + Time\_day_3$	3315	3.07
$Area\_surveyed_3 + Slope_2 + Speed_3 + Date_3 + Time\_day_3$	3315	3.07
Poaching hypothesis		
$Area\_surveyed_3 + Distance\_urban_3 + Speed_3 + Date_3 + Time\_day_3$	3233	0
$Area\_surveyed_3 + Distance\_urban_3 + Speed_3 + Date_3 + Time\_day_2$	3234	1.66
$Area\_surveyed_3 + Distance\_urban_3 + Distance\_oil + Speed_3 + Date_3 + Time\_day_3$	3235	1.96
$Area\_surveyed_2 + Distance\_urban_3 + Distance\_oil + Speed_3 + Date_3 + Time\_day_3$	3237	3.96
Sheep ranching hypothesis		
$Area\_surveyed_3 + Density\_sheep_3 + Speed_3 + Date_3 + Time\_day_3$	3280	0
$Area\_surveyed_2 + Density\_sheep_3 + Speed_3 + Date_3 + Time\_day_3$	3282	2.60
$Area\_surveyed_3 + Density\_sheep_3 + Speed_3 + Date_3 + Time\_day$	3284	3.37

For each model Akaike's Information Criteria (AIC) and the difference on AIC between the current model and the best model (Δ AIC) are given. *Numeric subscripts* refer to the df of splines

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