Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

Including species interactions in resource selection of guanacos and livestock in Northern Patagonia

N. M. Schroeder[1,2], R. Ovejero[1,2], P. G. Moreno[2,3], P. Gregorio[2], P. Taraborelli[1,2], S. D. Matteucci[4] & P. D. Carmanchahi[2]

1 CONICET, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Mendoza, Argentina
2 CONICET, GIEFAS-INIBIOMA-AUSMA-UNCo, San Martín de los Andes, Neuquén, Argentina
3 CONICET, ICiVet-Litoral, LEcEn, FCV-UNL, Santa Fe, Argentina
4 CONICET, GEPAMA-UBA, Buenos Aires, Argentina

Keywords
species interactions; resource selection; *Lama guanicoe*; livestock; arid lands.

Correspondence
Natalia Mariel Schroeder, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), CONICET, Av. Ruiz Leal s/n, Parque General San Martín, Mendoza Ciudad, CC 507, CP 5500, Argentina. Tel: 54 261 5244166; Fax: 54 261 5244001
Email: natalias@mendoza-conicet.gob.ar

Editor: Jane Waterman

Received 22 January 2013; revised 25 June 2013; accepted 28 June 2013

doi:10.1111/jzo.12065

Abstract

Species occurrence depends on both environmental and biotic factors (species interactions). Consideration of species interactions when estimating functions of population distribution is unusual, and may be crucial to understand and predict how species use space and resources. In this study, we combine resource selection probability functions (RSPFs) with a model selection approach based on information theory to evaluate how biotic (interspecific interactions) and abiotic (environmental) factors affect resource selection of guanacos *Lama guanicoe* and livestock (goats, sheep, cattle and horses) in two seasonal periods. We first test different *a priori* hypotheses of the environmental effects on guanacos and livestock occurrence (i.e. foraging, predation/topography and human effect hypotheses), then we assess model performance with independent data, and finally we use validated models of each species as predictors of the interaction between them. In all seasons, *L. guanicoe* occurrence was influenced by both environment and livestock interactions, especially small livestock (goats and sheep). Guanacos selected for habitats characterized by high temporal variability in plant productivity and away from potential human contact. In all seasons, *L. guanicoe* was negatively related to the RSPF of small livestock, but the reverse was not the case, suggesting that *L. guanicoe* avoids sites used by goats and sheep. In contrast, livestock was mainly affected by environmental variables related to human presence and was not affected by the interactions with herbivores. Contrary to our predictions, goats and sheep were also associated with less productive sites, probably indicating strong degradation of the sites to which they are restricted. Our results suggest a spatial segregation between *L. guanicoe* and domestic herbivores throughout the year, which is explained by competitive interactions of *L. guanicoe* with small livestock but also in response to vegetation productivity and human pressure. This study shows the importance of including species interaction effects in habitat modeling.

Introduction

Understanding the factors that govern the distribution and abundance of species has been a constant motivation among ecologists (e.g. Wiegand, Gunatilleke & Gunatilleke, 2007). Essentially, species occurrence depends on both first-order and second-order factors. The former are related to habitat preferences, where the occurrence of a species depends on environmental variables, such as food availability, shelter, altitude and disturbance. Second-order factors refer to biotic interactions with other species, whether competitors, predators or facilitators (Wiegand *et al*., 2007). Overall, consideration of environmental factors has prevailed in the study of species distribution and occurrence (McLoughlin *et al*., 2010). Despite decades of study on density-dependent habitat selection, and the key role of competitive and predator–prey interactions (e.g. Chase *et al*., 2002; Morris, 2003), these issues are usually not considered when estimating functions of population distribution and habitat use (Milesi & Lopez de Casenave, 2005, McLoughlin *et al*., 2010). Not considering biotic interactions could overestimate the total area truly available to species, and ultimately affect derived management recommendations for mitigating negative effects on species distribution.

The guanaco *Lama guanicoe* and domestic herbivores share a large area of arid land in south-western South America. According to diet and body size, Puig *et al.* (2001) grouped guanacos (100–120 kg), goats (50 kg) and sheep (50 kg) as small grazer-browser ungulates, while horses (300 kg) and cattle (350 kg) are classified as large strictly grazer ungulates. According to this study, *L. guanicoe* overlaps its diet by 68% with horses, 56% with cattle, 48% with goats and 82% with sheep, indicating a potential for competition between the native species and livestock, mainly sheep (Baldi *et al*., 2004). Where the human pressure is low, *L. guanicoe* is associated with high availability of preferred forage (Puig *et al*., 1996, 2008) and it shifts to low productivity sites (suboptimal) when sheep are present at high densities monopolizing most productive areas (Baldi, Albon & Elston, 2001; Baldi *et al*., 2004; Pedrana *et al*., 2010). Some authors have found that *L. guanicoe* prefers flat open areas where it is easier to detect and escape from predators with an ambush hunting strategy, such as *Puma concolor* (Puig *et al*., 2008; Taraborelli *et al*., 2012), although other results also showed an opposite pattern (Pedrana *et al*., 2010). These authors interpret that the association of *L. guanicoe* with rugged terrain and steep slopes, as well as low productivity, may not reflect true habitat preferences but an indirect response to its negative interaction with sheep (Baldi *et al*., 2001; Pedrana *et al*., 2010).

Most studies of resource selection of *L. guanicoe* in interaction with livestock have focused on central and south Patagonia, where livestock raising is almost exclusively of sheep at high densities, with fences restricting seasonal movements of guanaco (Rey, Novaro & Guichón, 2012). Currently, empirical data about resource selection of guanaco and other domestic herbivores such as goats, cattle and horses living in simpatry in unfenced places, are limited. Differences in seasonal forage availability could lead to changes in diet (Puig *et al*., 1996), promote migratory behavior (Fryxell & Sinclair, 1988) and ultimately generate seasonal habitat use pattern. Also, this important issue has received little attention. The few existing studies have focused only on native species, restricted to small spatial scales in relation to ungulates movements, conducted in one season, and/or have used indirect evidence of habitat use (feces) (Ovejero *et al*., 2011; Acebes, Traba & Malo, 2012).

The aim of this work was to evaluate how biotic (interspecific interactions) and abiotic (environmental) factors affect resource selection of *L. guanicoe* and livestock (cattle, horses, goats and sheep) in two seasonal periods. We combine resource selection functions (Manly *et al*., 2002) with a model selection approach based on information theory (Burnham & Anderson, 2002). We first test different *a priori* hypotheses of the environmental effects on guanacos and livestock occurrence (i.e. foraging, predation/topography and human effect hypotheses; Table 1), then we assess model performance with independent data, and finally we use validated models of each species as predictors of the interaction between them.

Material and methods

Study area

The study area was located in northern Patagonia, central-west of Argentina (between 36°00′ and 36°36′S, and 68°34′ and 69°23′W), including part of the 664 100-ha La Payunia Reserve area. It is dominated by a gently undulating relief and vast flatlands, combined with steeper hills and volcanic outcrops. Temperatures average 6°C (winter) and 20°C (summer); annual precipitation is scarce (198 mm). Precipitation occurs in summer and winter (mainly snow), which, in combination with temperature, defines two periods of relatively high (summer) and low (winter) plant productivity. The vegetation is xerophytic, with 58% of coverage, belonging to La Payunia phytogeographic province within the Andean–Patagonian domain (Martínez Carretero, 2004). Sandy plains are covered by herbaceous communities dominated by *Panicum urvilleanum*, *Stipa speciosa* and *Sporobolus rigens*, while slopes and basaltic scoria present shrub communities mainly of *Neosparton aphyllum* and *Ephedra ochreata.* Main native herbivores are *Lama guanicoe*, *Pterocnemia pennata* and *Lagostomus maximus*. There are few human groups inhabiting the study area. Main productive activity is livestock raising, mainly goats, and also cattle, horses and sheep.

Data collection and sightability

Based on a preliminary survey, we selected an area of about 1200 km^2 following a grazing intensity gradient (from areas with abundant livestock presence to areas with no grazing activity) and with about 80% of roads and tracks available in the area. Vegetation structure in Patagonia is highly patchy, with high-cover vegetation patches ranging between 1- and 100-m diameter surrounded by areas with high proportion of bare soil (Aguiar & Sala, 1999). The result is an open and closed grassland–shrubland mosaic, of fuzzy edges, making it difficult to conduct a stratified sampling design. We assume that by following an intensive sampling design on existing roads, we cover the landscape heterogeneity.

Ground surveys of herbivores were made traveling on accessible roads and tracks, totaling the same 180 km of transects per visit. We followed the line transect method (Thomas *et al*., 2010), consisting of observations from a pick-up vehicle driven at low speed. For each group of animals encountered, we recorded the number of guanacos, type and number of livestock (goats, cattle, sheep, horses), distance and angle from the observer to the group measured with a laser rangefinder and compass, respectively, bearing to the north and geographic position with Global Positioning System. We made a total of nine surveys: two austral springs (October 2008, December 2009), two summers (January 2009 and February 2010), two falls (April 2009, May 2010) and three winters (June and September 2009, July 2010), corresponding to 47 days of fieldwork, and a sampling effort of 470 h. We obtained 3449 groups of animals (2541 groups of guanacos, 566 of cattle, 262 of horses, 55 of goats and 24 of sheep).

With the geographic position, distance and bearing to the north, we calculated the actual position of each observation. According to Puig *et al.* (2001), we grouped cattle and horses as large livestock and goats and sheep as small livestock. Models based on used/unused data require defining units (or cells) occupied by animals and unoccupied units. In this study, we used a 1-km spatial resolution as unit cell (defined by resolution of vegetation dataset; Table 2) to represent patches within home ranges (third-order selection; Johnson, 1980). We

Table 1 Hypotheses and predictions used to contrast *a priori* models based on the knowledge of *Lama guanicoe*, livestock and other similar herbivores, and predictor variables with codes used for each case

Hypotheses description and references	Predictions	Predictor variables and codes
1. Foraging		
More productive environment, proximity to water and north-facing slopes (aspect) are associated with better quality and availability of forage for ungulates. These traits largely determine habitat selection of herbivores (Baldi *et al.*, 2001, 2004; Puig *et al.*, 2001; Sawyer *et al.*, 2007; Pedrana *et al.*, 2010).	We predict higher probability of finding all herbivores at sites characterized by maximum plant productivity, close to watercourses and northerly aspect.	Vegetation productivity: *evi_annual_max, evi_annual_mean, evi_sum_max, evi_sum_mean, evi_win_max, evi_win_mean*. Vegetation heterogeneity: *evi_annual_cv, evi_sum_cv, evi_win_cv*. Temporary watercourses: *dist_river*. Aspect: *aspect*
2. Predation		
Steep slopes and rugged terrain are physical obstructions to visibility and escape strategy, and can increase predation risk for *L. guannicoe* affected by predators with an ambush hunting strategy, like cougars (Puig *et al.*, 2008).	We predict higher probability of finding *L. guanicoe* at flat open habitats and gentle slopes.	*elevation* *slope*
3. Topography		
While cattle and horses are restricted to flat and low slope habitats (Stewart *et al.*, 2002), goats and sheep could access to steep terrain, as has been observed for wild goats (*Oreamnos americanus*; Shafer *et al.*, 2012).	We predict higher probability of finding (3.a) cattle and horses at flat areas and gentle slopes; (3.b) goats and sheep at rugged terrains and steep slopes.	*elevation* *slope*
4. Human effect		
Habitats associated to human presence are detrimental to *L. guanicoe* due to high hunting pressure and persecution by settlers (Ogutu *et al.*, 2010; Pedrana *et al.*, 2010), while they benefit livestock because it allows access to water and care by people (Turner & Hiernaux, 2002; Ogutu *et al.*, 2010).	We predict higher probability of finding (4.a) *L. guanicoe* in areas of low poaching level, away from human settlements, and in public lands; (4.b) livestock in sites close to human settlements and private fields.	Permanent human settlements: *dist_perm* Temporary human settlements*: dist_temp* Land tenure: *lten* Poaching index: *poach*
5. Combined effects		
Resource selection of guanacos and livestock is determined by a combination of foraging, predation/topography and human effects.		
6. Interactions		
Herbivores of similar body weight and diet are expected to compete for food resources when they are in simpatry (De Boer & Prins 1990).	We predict (6.a) greater spatial segregation and negative correlation between *L. guanicoe* and selection function (RSPF) of small livestock, and (6.b) lower spatial segregation and lack of correlation between these species and the RSPF of large livestock.	Probability of use: *RSPFguanaco*, *RSPFlarge*, *RSPFsmall*.

calculated the effective sampled area (Supporting Information Appendix S1) to minimize the likelihood that cells with 0 values were in fact cells with undetected individuals. Following the methodology proposed by Travaini *et al.* (2007), we overlaid 1-km grid cell with the effective sampled area and selected those cells that overlapped completely or partially. We obtained a total of 378 cells for *L. guanicoe* and large livestock, and 411 cells for small livestock. The re-projected records of individuals were overlaid with selected cells. Cells with at least one record were considered ‘used’ (=1) and the rest were considered ‘unused’ (=0). We followed this procedure independently for each species (or species group in the case of livestock) and survey. The greater the proportion of 1-km surveyed cells, the higher the probability of detecting animals inside. We calculated the fraction of the cell surface overlapping with the effective sampled area (prop_area) and included it as fixed term in the models to compensate for its effect on probability of detection (Travaini *et al.*, 2007).

Selecting data for construction and validation of models

For *L. guanicoe* and large livestock, we grouped data of October 2008, December 2009 and February 2010 for construction of the spring–summer models. To control for pseudo-replication and temporal autocorrelation, we overlaid

Table 2 Description of the predictor variables used in the analysis

Variable	Code	Description
Plant productivity	evi_annual_max evi_annual_mean evi_sum_max evi_sum_mean evi_win_max evi_win_med	Maximum and mean value of enhanced vegetation index (EVI) in 10 years (2001–2011) at 1-km spatial resolution. These variables were calculated for the whole year, for summer months of maximum productivity (February–March) and winter months of minimal productivity (August–September).
Temporal variability of plant productivity	evi_annual_cv evi_sum_cv evi_win_cv	Coefficient of variation of EVI in 10 years (2001–2011) at 1-km spatial resolution. This variable was calculated for the whole year, for summer months of maximum productivity (February–March) and winter months of minimal productivity (August–September).
Distance from temporary watercourses	dist_river	Euclidean distance to temporary watercourses in the study area
Elevation	elevation	Elevation of 1-km cells in meters (from original 90-m grid)
Aspect	aspect	Slope exposure (north, south, east, west) estimated from the elevation data
Slope	slope	Slope (percentage) estimated from elevation data
Distance from permanent human settlements	dist_perm	Euclidean distance to permanent human settlements
Distance from temporary human settlements	dist_temp	Euclidean distance to temporary human settlements
Land tenure	lten	Cadastral map with boundaries of private and public fields
Poaching index	poach	Poaching index map (high = 3, low = 1) for study area. Conservation values were first identified as animal species important for conservation. Threats associated with each value were also categorized and prioritized according to extension, duration and intensity. The index was constructed (and mapped) by weighing the number of illegal actions (poaching with guns or dogs, carrying firearms, cross-country movements) and the conservation value of specific area.
Probability of use	RSPFguanaco RSPFlarge RSPFsmall	Probability of use by guanaco, large and small livestock, based on the best fitted model (see text for details)

the different surveys of this seasonal period and classified the 1-km cells as used or unused in at least one survey. The January 2009 survey was subsequently used for validation (see below). Similarly, we selected surveys of April 2009, September 2009, May 2010 and July 2010 to build the fall–winter models, and used the June 2009 survey for validation. This data grouping procedure allowed us to increase the sample size of used cells while analyzing two seasonal periods of different plant productivity. Due to the low number of observations, in the case of small livestock, we randomly selected 80% of data for the annual model construction, leaving the remaining 20% to validate it. The number of used and unused cells considered for the construction of models was: for *L. guanicoe*: used = 223, unused = 155 (spring–summer), used = 187, unused = 191 (fall–winter); for large livestock: used = 96, unused = 282 (spring–summer), used = 132, unused = 246 (fall–winter), and for small livestock: used = 25, unused = 304 (annual).

Environmental variables

We identified 17 variables as potential landscape predictors of guanacos and livestock resource selection summarized in Table 2. We acquired the enhanced vegetation index (EVI) from the MODIS satellite imagery seasonal database at 1-km spatial resolution (https://lpdaac.usgs.gov/products/modis_products_table). Temporary watercourses were obtained from the National Geographic Institute database. We used IDRISI Taiga 16.05 software to calculate mean elevation, slope and aspect from a digital elevation model at obtained from the Global Land Cover Facility of University of Maryland (http://glcf.umd.edu/). Location data of permanent and temporary human settlements come from own records and rangers' information. Land tenure was acquired from the provincial land ownership register. The poaching index map was obtained from a Control and Monitoring Hunting Program initiated in 2009 by rangers using historical (n = 324) and current (n = 2241) records of procedures and road controls from 1996 to 2011 (L. Aros and D. Quiroga park rangers, pers. comm.).

Model fitting and selection

We used the method of model selection from combinations of the predictor variables proposed by Burnham & Anderson (2002). We grouped environmental variables according to various hypotheses (Table 1). Mean EVI in all seasonal periods and the rest of EVI variables in the maximum productivity period were excluded from analysis due to multicollinearity issues (Pearson's pairwise correlation analysis, $|r| > 0.6$).

A generalized linear model based on logistic regression was used to estimate resource selection probability function (RSPF) for each hypothesis and species (or species group). The RSPF provides an estimate of the probability of herbivores selecting a location given its habitat characteristics. We considered quadratic terms for elevation, slope and distance during the model-building process. Aspect was transformed to categorical variable: N, E, S, W (and A when slope = 0, for reference level). Models were compared using the Bayesian information criterion (BIC; Burnham & Anderson, 2002), recommended for large sampled sizes. We considered as competing models those whose ΔBIC value was <2.0. Finally, we built a 'general model' with all relevant variables retained in the most parsimonious model for each hypothesis. All models were fitted using R package *stats* (http://www.r-project.org/).

Model validation

To validate the most parsimonious model (hereafter 'final model'), we used the method recommended by Boyce *et al.* (2002) and adapted by Coe *et al.* (2011) for independent datasets and cells as sample unit. We predicted probability of selection for each 1-km cell using the final model and the independent dataset. We sorted cells by predicted probability of use, from low to high, and we placed the values in 20 bins (equal numbers of cells in each). We counted the number of used cells in each bin, and finally we used Spearman's rank correlation (r_s) to test the relationship between bin rank and number of used cells. The predictive model should have a correlation of ≥0.7 to be considered valid.

Species interactions

We followed the Johnson *et al.* (2000) approach to assess interspecific interactions. We used the final 'specific' RSPF model (only constructed with environmental variables), as predictor variable of interaction effect in a new resource selection function of herbivores (interspecific models). We performed this procedure for each species (or species group) and season. For example, for *L. guanicoe* in spring–summer period, we obtained three interspecific models: one with the large livestock RSPF, one with the small livestock RSPF and one with RSPFs of both small and large livestock. Interspecific and specific models were then compared by BIC.

Results

Specific models

For *L. guanicoe*, the final model in spring–summer combined effects under different hypotheses (foraging, predation and human effect; Table 3). The species selected sites that show higher productivity variability in time (CV of EVI > 0.25), lower slope, high elevation sites (>1700 m), away from temporary human settlements and up to 10 km away from permanent human settlements (Fig. 1a). Correlation between probability of selection predicted by the final model and used cells in independent data was high ($r = 0.91$). In fall–winter, the model of best fit supported the human effect hypothesis, although the model that also included variability in productivity and elevation had equal fit (model gfwgen1, ΔBIC < 2; Table 3). The validation test was higher for the first model (gfwhum12: $r_s = 0.71$, gfwgen1: $r_s = 0.68$), so we selected it as the final model. In fall–winter, therefore, guanacos were associated with sites up to 10 km away from permanent human settlements, but nearer to temporary human settlements, and with low poaching pressure (Fig. 1b).

In both seasonal periods, the best models for large livestock were those of the human effect hypothesis (Table 4). Cattle and horses selected sites near permanent human settlements (<5 km; Fig. 2a,b), while in fall–winter, they were also associated with private parcels and temporary human settlements (<10 km; Fig. 2b). The validation value in spring-summer was $r_s = 0.73$, while in fall–winter, it was $r_s = 0.90$.

For small livestock, the annual model of best fit supported the combined effects hypothesis (Table 5). Goats and sheep selected sites very close to permanent human settlements (<3 km), associated with private parcels. They also used low elevation (<1400 m) and low annual maximum productivity sites (<0.15; Fig. 3).

Species interactions

In spring–summer, *L. guanicoe* final model improved after including the final RSPF for small livestock as predictor, and the new validation value was also high (Table 6). The coefficient of this variable was negative ($\beta = -2.643$; Supporting Information Table S1). Similarly, in fall–winter, guanaco final model improved after including the final RSPF for both small and large livestock (Table 6). In this case, *L. guanicoe* was negatively related to small livestock ($\beta = -2.107$), but positively related to large livestock ($\beta = 0.2483$; Supporting Information Table S1).

Final model of large and small livestock did not improve with the addition of any specific final model (Table 6).

Discussion

Human variables had negative effect on *L. guanicoe* resource selection in both seasonal periods, clearly supporting our hypothesis. This species occurred far from human settlements, associated with public lands (spring–summer) and with low poaching pressure (fall–winter). As there are no fences in our study area, land tenure is an indicator of the presence and quantity of human settlements. Our results suggest that human activity, whether expressed as hunting pressure or direct persecution, has a negative impact on *L. guanicoe*. Disturbance related to human presence has been described for *L. guanicoe* by Donadio & Buskirk (2006), Baldi *et al.* (2010) and Pedrana *et al.* (2010). Legal and illegal hunting are of major concern for guanaco conservation. In La Payunia, guanaco poaching decreased in intensity after the creation of the natural reserve in 1982. However, our data suggest that *L. guanicoe* retains an evasive response to sites with high poaching pressure, as was observed in other protected areas of

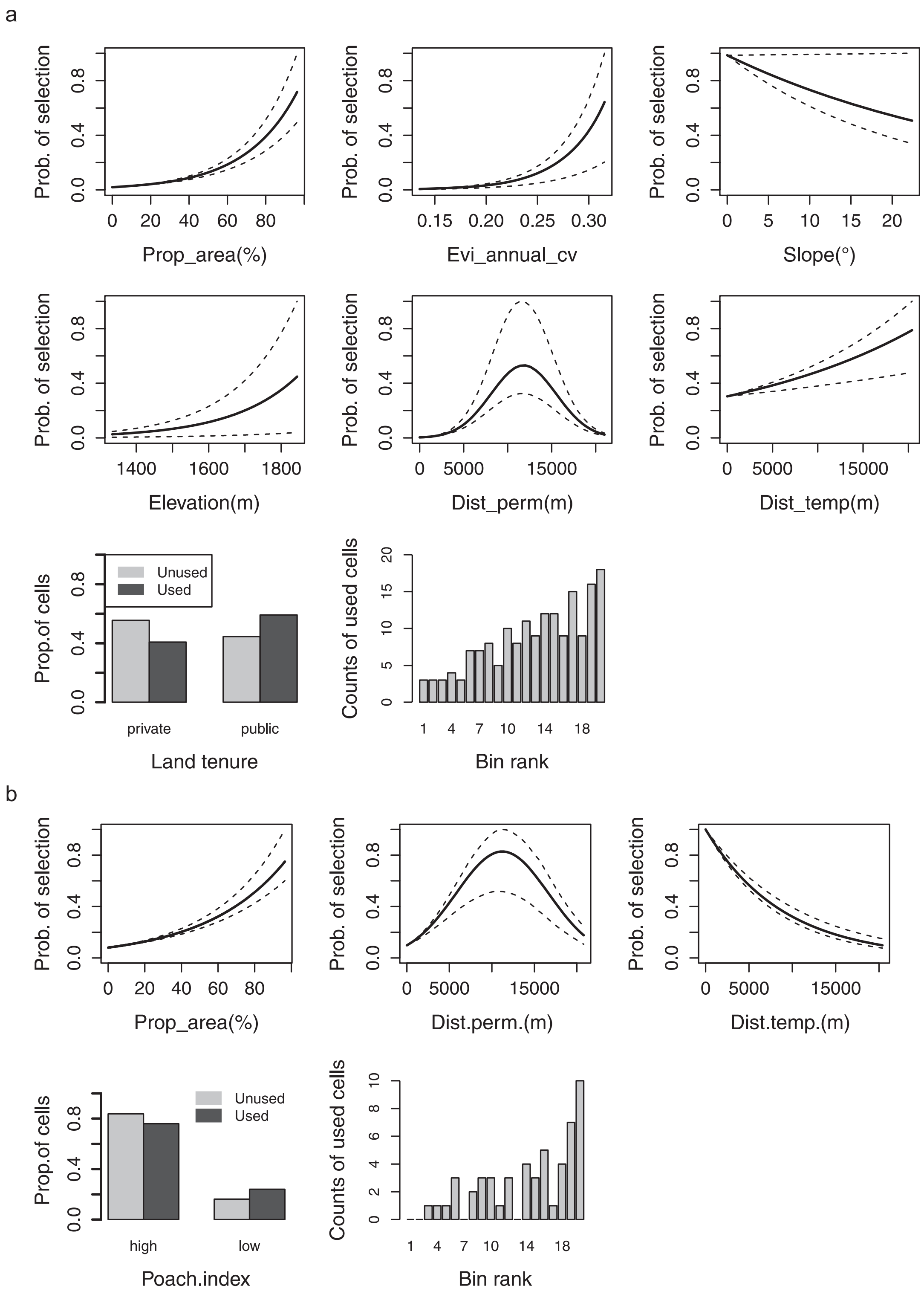

Figure 1 Marginal plots showing probability of selection for predictors of the specific model for *Lama guanicoe* in (a) spring–summer and (b) fall–winter (Table 3). In each plot, all other variables were held constant at their respective median. Dashed lines represent 90% confidence intervals for the mean effect, calculated by resampling (with replacement) a random subset of data (replicates = 1000). It also shows the proportion of used and unused cells for land tenure categories (public and private) in (a), the proportion of used and unused cells for poaching index categories (high and low) in (b), and the validation plot with independent data (January 2009 for spring–summer, June 2009 for fall–winter). The number of used cells are highly correlated with the probability of selection (expressed as increased bins) predicted by the corresponding model.

Table 3 Summary of resource selection probability function models for *Lama guanicoe* in spring–summer and fall–winter, for each hypothesis. Bayesian information criterion (BIC), the difference between each model and the most parsimonious model (ΔBIC), and relative weight (W_i) are given. Most parsimonious models (lower BIC) are highlighted in bold type

Hypothesis	Code	Models (direction of effect '+' or '–')	BIC	ΔBIC	W_i
Spring–summer					
Foraging	gpsfor1	prop_area (+), evi_annual_cv (+)	439.5	32.8	<0.001
	gpsfor7	prop_area (+), evi_annual_cv (+), evi_annual_max (+), evi_win_cv (–), evi_win_max (–)	441.1	34.4	<0.001
	gpsfor11	prop_area (+), evi_annual_cv (+), evi_win_cv (–), evi_win_max (–), dist_river (–)	440.5	33.8	<0.001
Predation	gpspred5	prop_area (+), elevation[a] (+/–), slope (–)	475.6	68.9	<0.001
Human effect	gpshum11	prop_area (+), dist_perm[a](+/–), dist_temp (+), lten.public (+),	432.4	25.7	<0.001
Combined effects	gpsgen1	prop_area (+), evi_annual_cv (+), elevation[a] (–+), slope (–), dist_perm[a] (+/–), dist_temp (+), lten.public (+)	411.3	4.6	0.09
	gpsgen2	**prop_area (+), evi_annual_cv (+), elevation (+), slope (–), dist_perm[a] (+/–), dist_temp (+), lten.public (+)**	**406.7**	**0**	**0.90**
	gpsgen3	prop_area (+), evi_annual_cv (+), slope (+), dist_perm[a] (+/–), dist_temp (+), lten.public (+)	416.4	9.7	0.01
Fall–winter					
Foraging	gfwfor1	prop_area (+), evi_annual_cv (+)	504.1	13.4	<0.001
	gfwfor2	prop_area (+), evi_annual_max (+)	502.8	12.1	0.001
Predation	gfwpred1	prop_area (+), elevation (+)	506.6	15.9	<0.001
	gfwpred7	prop_area (+), elevation[a] (+/–)	505.9	15.2	<0.001
Human effect	**gfwhum12**	**prop_area (+), dist_perm[a](+/–), dist_temp (–), poach.high (–)**	**490.7**	**0.0**	**0.53**
Combined effects	gfwgen1	prop_area (+), evi_annual_cv (+), elevation(+), dist_perm[a] (+/–), dist_temp (–), poach.high (–)	492.0	1.3	0.27
	gfwgen2	prop_area (+), evi_annual_cv (+), elevation[a] (–+), dist_perm[a] (+/–), dist_temp (–), poach.high (–)	497.5	6.9	0.02
	gfwgen3	prop_area (+), evi_annual_max (–), elevation (+), dist_perm[a] (+/–), dist_temp (–), poach.high (–)	493.0	2.3	0.17
	gfwgen4	prop_area (+), evi_annual_max (+), elevation[a] (–+),dist_perm[a] (+/–), dist_temp (–), poach.high (–)	498.8	8.1	0.0

[a] Quadratic term.

western Argentina (Donadio & Buskirk, 2006). Some of our surveys were conducted on roads frequently associated with access to hunters. However, we also surveyed internal tracks of hard walk-ability, avoided by poachers. Consequently, our analysis reflects selection pattern of guanacos in a poaching intensity gradient associated with roads.

Human settlements are usually associated with sites of high quality pasture and water availability. However, grazing pressure and trampling of vegetation by livestock close to settlements could be very high. Gradients of increasing forage biomass away from human settlements probably create optimal forage conditions at intermediate distances as a result of a trade-off between quality and quantity of food (Fryxell, 1991; Wilmshurst *et al.*, 1999). This may explain the 'humped' distribution observed for *L. guanicoe* in both seasonal periods, as tested with empirical data for other native herbivores in East Africa (Ogutu *et al.*, 2010).

Lama guanicoe was associated with sites of high temporal variability of plant productivity. This was clear in spring–summer. In fall–winter, this variable was present in the second best competitive model, also with a positive effect. This result may reflect that guanaco could access to habitats that occasionally are highly productive rather than to consistently unproductive sites, as was found in other similar studies at regional scale of extreme southern Patagonia for the same species (Travaini *et al.*, 2007; Pedrana *et al.*, 2010). Habitats with maximum annual values of plant productivity seem to be selected by guanacos in both seasonal periods (see variable evi_annual_max present in other competitive models inside foraging hypothesis in Table 3), but this selection is not observed when plant productivity is combined with other factors. Smaller scale studies conducted in La Payunia region demonstrated that guanacos select habitats with high availability of preferred plant species (Puig *et al.*, 2008), and that it has the capacity of alternating seasonally between grazing and browsing, according to forage availability (Puig *et al.*, 1996). This, in turn, is contrary to Baldi *et al.* (2001) findings in the central Patagonia, where guanacos are

Table 4 Summary of resource selection probability function for large livestock in spring–summer and fall–winter, for each hypothesis. Bayesian information criterion (BIC), the difference between each model and the most parsimonious model (ΔBIC) and relative weight (W_i) are given. Most parsimonious models (lower BIC) are highlighted in bold type

Hypothesis	Code	Models (direction of effect '+' or '–')	BIC	ΔBIC	W_i
Spring-summer					
Foraging	vepsfor1	prop_area (+), evi_annual_cv (–)	420.9	69.2	<0.001
	vepsfor3	prop_area (+), evi_annual_cv (–), evi_annual_max (+),	420.5	68.8	<0.001
	vepsfor10	prop_area (+), evi_annual_cv (–), dist_river (+)	421.7	70.0	<0.001
	vepsfor22	prop_area (+), evi_annual_cv (–), evi_annual_max (+), dist_river[a] (+/–)	420.7	69.0	<0.001
Topography	vepstopo7	prop_area (+), elevation[a] (–+)	400.8	49.1	<0.001
Human effect	**vepshum1**	**prop_area (+), dist_perm(–),**	**351.7**	**0.0**	**1.00**
Combined effects	vepsgen1	prop_area (+), evi_annual_cv (–), elevation[a] (+/–), dist_perm(–),	367.6	16.0	<0.001
	vepsgen2	prop_area (+), evi_annual_cv (–), evi_annual_max (+), elevation[a] (+/–), dist_perm (–),	373.4	21.8	<0.001
	vepsgen3	prop_area (+), evi_annual_cv (–), dist_river (+), elevation[a] (+/–), dist_perm (–),	365.5	13.8	0.00
	vepsgen4	prop_area (+), evi_annual_cv (–), evi_annual_max (+), dist_river[a] (+/–), elevation[a] (+/–), dist_perm (–)	369.4	17.7	<0.001
Fall-winter					
Foraging	vefwfor4	prop_area (+), evi_win_max (+)	470.5	102.6	<0.001
	vefwtopo1	prop_area (+), elevation (+)	473.3	105.3	<0.001
Topography	vefwtopo 7	prop_area (+), elevation[a] (–+)	471.3	103.3	<0.001
Human effect	**vefwhum13**	**prop_area (+), dist_perm (–), dist_temp (–), lten.public (–)**	**367.9**	**0.0**	**0.99**
Combined effects	vefwgen1	prop_area (+), evi_win_max (–), elevation (+), dist_perm (–), dist_temp (–), lten.public (–)	376.6	8.7	0.01
	vefwgen2	prop_area (+), evi_win_max (–), elevation[a] (+/–), dist_perm (–), dist_temp (–), lten.public (–)	382.0	14.1	<0.001

[a] Quadratic term.

less abundant at sites with greater availability of two preferred grass species (*Stipa* sp. and *Poa* sp.), both in spring and in summer. Our results, together with those of Puig *et al.* (1996, 2008), suggest that food selection patterns of *L. guanicoe* in La Payunia differ from those found elsewhere in its distribution range, and that these differences should be interpreted in terms of the interaction with livestock, as discussed later.

Human variables proved to be the most important in predicting resource selection by domestic herbivores, especially in the case of large livestock. Vegetation productivity and topography showed little importance in cattle and horses habitat selection, during all seasons. There was also no relationship between these herbivores and temporary watercourses, as would have been expected for an arid region. In arid and semi-arid savannas of Africa, it has been observed that distance to water (Ogutu *et al.*, 2010) and to human settlements (Turner & Hiernaux, 2002) exert a controlling influence on livestock and wild ungulate distribution. However, when compared together, human settlements exert a relatively stronger influence on livestock distribution than water, resulting in animal densities that decrease exponentially away from settlements for all distances to water (Ogutu *et al.*, 2010). Permanent surface water is absent in the study area; the scarce rain-water temporarily flows or tends to accumulate in impervious soil depressions, as water points. Sparse human population has settled close to these few water sources. Then, human settlements may be masking the water influence on livestock habitat selection. Alternately, the variable we used to quantify the water influence may not adequately reflect the water availability in the landscape. Further analysis would be important to incorporate the distribution of temporary water reservoirs (i.e. water points) as a better predictor of water influence on herbivore resource selection.

Contrary to our expectations, goats and sheep were associated with less productive sites. It is unlikely that this reflects true habitat preferences, rather it seems to be more related to a trade-off between possibilities and restrictions that small livestock has to places with better forage. Our results show that small livestock occurs not farther away than 3 km of human settlements. Unlike large livestock that graze freely, goats and sheep are often herded every night by people to minimize predation by cougars. Consequently, in this area, human settlements function as grazing centers, the same as watering points (or piospheres) in other pastoral systems where animals return periodically (Todd, 2006). Given that there are over 9500 goats and sheep with a very restricted distribution throughout the year in the study area (Schroeder, 2013), it is assumed that there is a strong grazing pressure on these sites. Thus, goats and sheep would not be

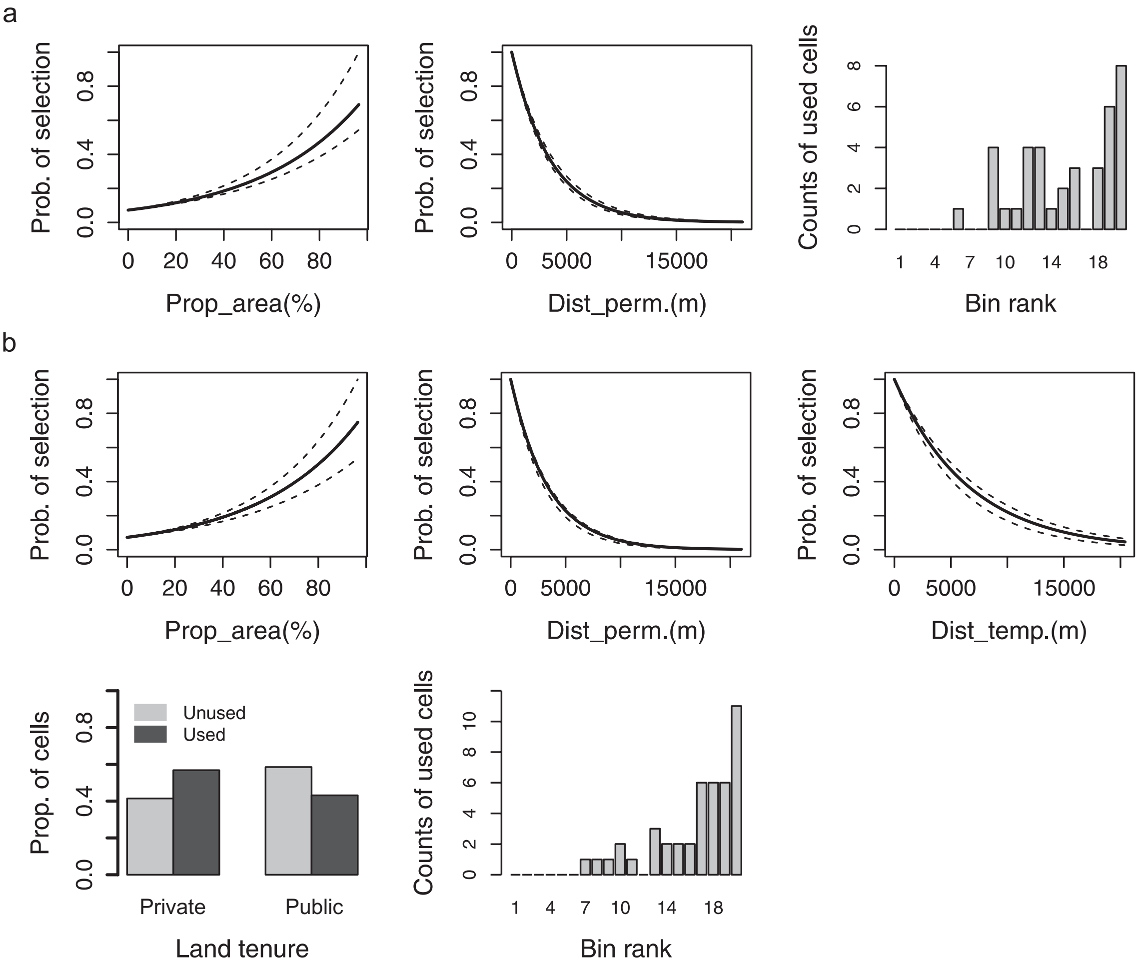

Figure 2 Marginal plots showing probability of selection for predictors of the specific model for large livestock in (a) spring–summer and (b) fall–winter (Table 4). In each plot, all other variables were held constant at their respective median. Dashed lines represent 90% confidence intervals for the mean effect, calculated by resampling (with replacement) a random subset of data (replicates = 1000). It also shows the proportion of used and unused cells for land tenure categories (public and private) in (b), and validation plot with independent data (January 2009 for spring–summer period, June 2009 for fall–winter). The number of used cells is correlated with the probability of selection (expressed as increased bins) predicted by the corresponding model.

Table 5 Summary of resource selection probability function for small livestock (annual period), for each hypothesis. Bayesian information criterion (BIC), the difference between each model and the most parsimonious model (ΔBIC) and relative weight (*W*ᵢ) are given. The most parsimonious model (lower BIC) is highlighted in bold type

Hypothesis	Code	Models (direction of effect '+' or '–')	BIC	ΔBIC	*Wi*
Annual					
Foraging	chofor1	prop_area (+), evi_annual_cv (–)	186.5	60.3	<0.001
	chofor2	prop_area (+), evi_annual_max (–)	186.0	59.9	<0.001
	chofor4	prop_area (+), evi_win_max (+)	187.3	61.1	<0.001
	chofor8	prop_area (+), dist_river (–)	186.9	60.8	<0.001
Topography	chotopo 7	prop_area (+), elevation[a] (–+)	155.8	29.7	<0.001
Human effect	chohum14	prop_area (+), dist_perm (–), lten.public (–)	147.1	21	<0.001
Combined effects	chogen1	prop_area (+), evi_annual_max (–), elevation[a] (–+), dist_perm (–), lten.public (–)	129.3	3.2	0.152
	chogen2	**prop_area (+), evi_annual_max (–), elevation (–), dist_perm (–), lten.public (–)**	**126.1**	**0.0**	**0.73**
	chogen3	prop_area (+), evi_win_max (–), elevation[a] (–+), dist_perm (–), lten.public (–)	129.8	3.7	0.117

[a] Quadratic term.

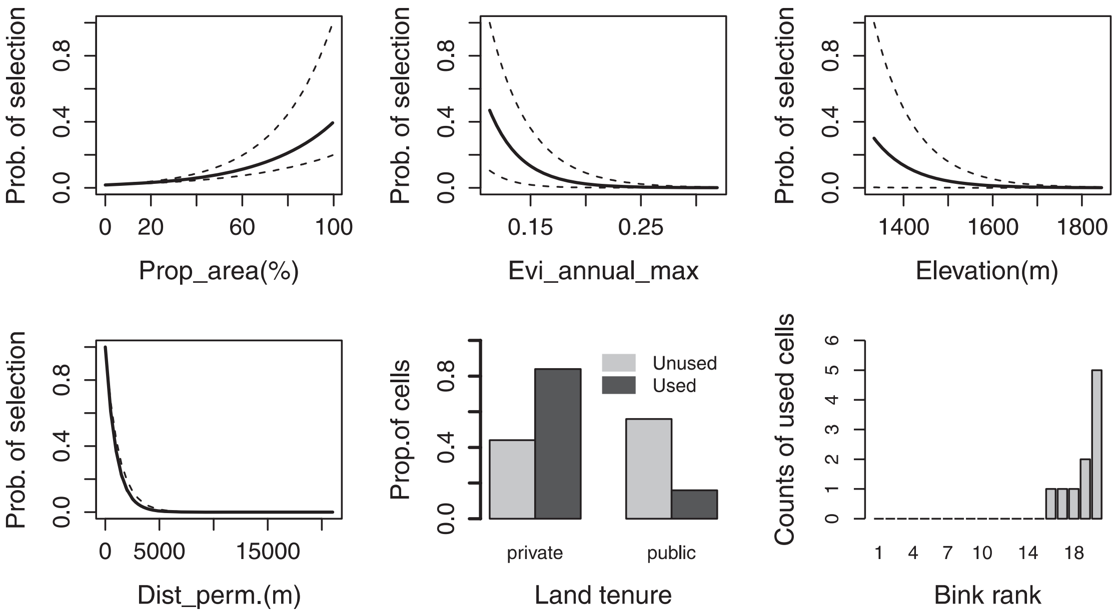

Figure 3 Marginal plots showing probability of selection for predictors of the specific model for small livestock (annual period) (Table 5). In each plot, all other variables were held constant at their respective median. Dashed lines represent 90% confidence intervals for the mean effect, calculated by resampling (with replacement) a random subset of data (replicates = 1000). It also shows the proportion of used and unused cells for land tenure categories (public and private), and validation plot with independent data (20% of total data). The number of used cells is correlated with the probability of selection (expressed as increased bins) predicted by the corresponding model.

selecting less productive sites, but instead they would cause a strong degradation of the sites to which they are restricted.

Specific models showed that *L. guanicoe* and domestic herbivores did not select resources similarly in both seasonal periods. They differed in how they select for distance to human settlements, land tenure, elevation and plant productivity. When they selected for the same variable, the coefficients had opposite signs. This shows that species select different habitat properties. If a species is spatially segregated from another, it should be inversely correlated with the resource selection of the other species (Johnson *et al.*, 2000). This prediction was proved for the interaction between guanaco and small livestock, in both seasonal periods: *L. guanicoe* was negatively related to the RSPF of goats and sheep, but the reverse is not the case, suggesting guanacos avoid sites used by goats and sheep. Our results show that potential for competition between *L. guanicoe* and small livestock, widely reported for the same species elsewhere in Argentina and Chilean Patagonia (Baldi *et al.*, 2001; Pedrana *et al.*, 2010), also occurs in this system throughout the year, even with stocking rates considerably lower than those recorded in the aforementioned sites. However, we cannot conclude about the mechanisms associated with these potential competitive interactions. Probably, *L. guanicoe* avoids goats and sheep because they deplete the available forage resources. This is supported by the fact that small livestock is associated with less productive sites. Besides, since goats and sheep graze in close proximity to human settlements, direct persecution and poaching of *L. guanicoe* by local people in these sites cannot be discarded. The elucidation of underlying mechanisms will require manipulative or experimental studies.

The interaction between guanacos and large livestock in fall–winter was not in line with our predictions. *Lama guanicoe* was positively associated with cattle and horses. One possible explanation arises, although it cannot be confirmed by our data. Food is limited in fall–winter, and animal movements are restricted to certain areas because higher elevations are covered with snow. Additionally, guanaco abundance in winter can be 6.5 times lower than the abundance achieved in spring (Schroeder, 2013) due to the migrating behavior. Thus, the probability of encountering guanacos in places where there are also cattle and horses could be a consequence of a reduced availability of suitable habitats, along with the avoidance of goats and sheep, favored by a low-density scenario. Further studies might provide useful insights.

Our results have important conservation and management implications as it allows one to identify the main factors that negatively affect guanaco distribution (such as poaching pressure or small livestock raising), necessary to establish priority management actions, while also it raises concerns about feasibility of sedentary livestock activity of high stocking rate in restricted areas.

Acknowledgments

We thank the park rangers for the information of poaching index. Many thanks to R. Nielson and M. Wisdom for the

Table 6 Comparison of specific and interspecific resource selection probability function for *Lama guanicoe* and livestock in both seasonal periods. Bayesian information criterion (BIC), the difference between each model and the most parsimonious model (ΔBIC), and Spearman's rank correlation coefficient (r_s) are given. Most parsimonious models (lower BIC) are highlighted in bold type. References: ps: spring–summer fw: fall–winter

Seasonal period	Models	BIC	ΔBIC	r_s
L. guanicoe				
Spring–summer	RSPFguanaco[a]	406.7	12.4	0.91
	RSPFguanaco + RSPFlarge[b]	410.7	16.4	
	RSPFguanaco + RSPFsmall[c]	**394.3**	**0.0**	**0.89**
	RSPFguanaco + RSPFlarge + RSPFsmall	399.7	5.4	–
Fall–winter	RSPFguanaco	490.7	11.7	0.71
	RSPFguanaco + RSPFlarge	495.8	16.8	–
	RSPFguanaco + RSPFsmall	481.5	2.6	–
	RSPFguanaco + RSPFlarge + RSPFsmall	**479.0**	**0.0**	**0.71**
Large livestock				
Spring–summer	**RSPFlarge**[b]	**351.7**	**0.0**	**0.73**
	RSPFlarge + RSPFguanaco[a]	355.4	3.7	–
	RSPFlarge + RSPFsmall[c]	356.5	4.8	–
	RSPFlarge + RSPFguanaco + RSPFsmall	360.3	8.7	–
Fall–winter	**RSPFlarge**	**367.9**	**0.0**	**0.90**
	RSPFlarge + RSPFguanaco	372.7	4.7	–
	RSPFlarge + RSPFsmall	373.9	5.9	–
	RSPFlarge + RSPFguanaco + RSPFsmall	378.5	10.6	–
Small livestock				
Annual	**RSPFsmall**[c]	**126.1**	**0.0**	**0.76**
	RSPFsmall + RSPFguanaco[a] (ps)	131.2	5.1	–
	RSPFsmall + RSPFlarge[b] (ps)	130.7	4.5	–
	RSPFsmall + RSPFguanaco (ps) + RSPFlarge (ps)	135.4	9.3	–
	RSPFsmall + RSPFguanaco (fw)	131.9	5.8	–
	RSPFsmall + RSPFlarge (fw)	129.6	3.5	–
	RSPFsmall + RSPFguanaco (fw) + RSPFlarge (fw)	135.3	9.2	–

[a] RSPFguanaco = model gpsgen2 (spring–summer) and model gfwhum12 (fall–winter; Table 3).

[b] RSPFlarge = model vepshum1 (spring–summer) and model vefwhum13 (fall–winter; Table 4).

[c] RSPFsmall = model chogen2 (Table 5).

assistance with habitat modeling, and two anonymous reviewers for their valuable comments. Nelly Horak helped with the English language. This study was partially financed by IDEA WILD, Sigma Xi, Cleveland Metro Park Zoo, ANPCyT (PICT-1305; 0084) and CONICET (PIP-11220100100386, fellowship to N.S.).

References

Acebes, P., Traba, J. & Malo, J.E. (2012). Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *J. Arid Environ.* **77**, 39–44.

Aguiar, M.R. & Sala, O.E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends Ecol. Evol.* **14**, 273–277.

Baldi, R., Albon, S.D. & Elston, D.A. (2001). Guanacos and sheep: evidence for continuing competition in arid Patagonia. *Oecologia* **129**, 561–570.

Baldi, R., Pelliza-Sbriller, A., Elston, D. & Albon, S.D. (2004). High potential for competition between guanacos and sheep in Patagonia. *J. Wildl. Mgmt.* **277**, 924–938.

Baldi, R., Novaro, A., Funes, M., Walker, S., Ferrando, P., Failla, M. & Carmanchahi, P. (2010). Guanaco management in Patagonian rangelands: a conservation opportunity on the brink of collapse. In *Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems*: 266–290. du Toit, J., Kock, R. & Deutsch, J. (Eds). Chichester: John Wiley & Sons.

Boyce, M., Vernier, P., Nielsen, S. & Schmiegelow, F. (2002). Evaluating resource selection functions. *Ecol. Modell.* **157**, 281–300.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M. & Case, T.J. (2002). The interaction between predation and competition: a review and synthesis. *Ecol. Lett.* **5**, 302–315.

Coe, P.K., Johnson, B.K., Wisdom, M.J., Cook, J.G., Vavra, M. & Nielson, R.M. (2011). Validation of elk resource selection models with spatially independent data. *J. Wildl. Manag.* **75**, 159–170.

De Boer, W.F. & Prins, H.H.T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82**, 264–274.

Donadio, E. & Buskirk, S. (2006). Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biol. Conserv.* **127**, 139–145.

Fryxell, J.M. (1991). Forage quality and aggregation by large herbivores. *Am. Nat.* **138**, 478–498.

Fryxell, J.M. & Sinclair, A.R.E. (1988). Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* **3**, 237–241.

Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L. & Kie, J.G. (2000). Resource selection and spatial separation of mule deer and elk during spring. *J. Wildl. Mgmt.* **64**, 685–697.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals: statistical analysis and design for field studies*. 2nd edn. Boston: Kluwer Press.

Martínez Carretero, E. (2004). La provincia fitogeográfica de la payunia. *Bol. Soc. Argent. Bot.* **39**, 195–226.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering ecological dynamics in resource selection functions. *J. Anim. Ecol.* **79**, 4–12.

Milesi, F. & Lopez de Casenave, J.L. (2005). El concepto de nicho en Ecología aplicada: del nicho al hecho hay mucho trecho. *Ecol. Austral.* **15**, 131–148.

Morris, D.W. (2003). Toward an ecological synthesis: a case for habitat selection 1–13.

Ogutu, J.O., Piepho, H., Reid, R.S., Rainy, M.E., Kruska, R.L., Worden, J.S., Nyabenge, M. & Hobbs, N. (2010). Large herbivore responses to water and settlements in savannas. *Ecol. Monogr.* **80**, 241–266.

Ovejero, R.J., Acebes, P., Malo, J.E., Traba, J., Mosca Torres, M.E. & Borghi, C.E. (2011). Lack of feral livestock interference with native guanaco during the dry season in a South American desert. *Eur. J. Wildl. Res.* **57**, 1007–1015.

Pedrana, J., Bustamante, J., Travaini, A. & Rodríguez, A. (2010). Factors influencing guanaco distribution in southern Argentine Patagonia and implications for its sustainable use. *Biodivers. Conserv.* **19**, 3499–3512.

Puig, S., Videla, F., Monge, S. & Roig, V. (1996). Seasonal variations in guanaco diet (*Lama guanicoe* Muller 1776) and food availability in Northern Patagonia, Argentina. *J. Arid Environ.* **34**, 215–224.

Puig, S.,Videla, F., Cona, M.I. & Monge, S. (2001). Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). *J. Arid Environ.* **47**, 291–308.

Puig, S., Videla, F., Cona, M.I. & Roig, V.G. (2008). Habitat use by guanacos (*Lama guanicoe*, Camelidae) in northern Patagonia (Mendoza, Argentina). *Stud. Neotrop. Fauna Environ.* **43**, 1–9.

Rey, A., Novaro, A.J. & Guichón, M.L. (2012). Guanaco (*Lama guanicoe*) mortality by entanglement in wire fences. *J. Nature Conserv.* **20**, 280–283.

Sawyer, H., Nielson, R.M., Lindzey, F.G., Keith, L., Powell, J.H. & Abraham, A.A. (2007). Habitat selection of Rocky Mountain elk in a nonforested environment. *J. Wildl. Mgmt.* **71**, 868–874.

Schroeder, N. (2013). *Interacción entre el guanaco (*Lama guanicoe*) y herbívoros domésticos en el paisaje de La Payunia (sur de Mendoza, Argentina)*. PhD thesis, Universidad Nacional de Cuyo, Mendoza.

Shafer, A.B.A., Northrup, J.M., White, K.S., Boyce, M.S., Côté, S.D. & Coltman, D.W. (2012). Habitat selection predicts genetic relatedness in an alpine ungulate. *Ecology* **93**, 1317–1329.

Stewart, K.M., Bower, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. (2002). Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammal.* **83**, 229–244.

Taraborelli, P., Gregorio, P., Moreno, P., Novaro, A. & Carmanchahi, P. (2012). Cooperative vigilance: the guanaco's (*Lama guanicoe*) key antipredator mechanism. *Behav. Processes* **91**, 82–89.

Thomas, L., Buckland, S.T., Rexstad, E., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R., Marques, T. & Burnham, K.P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* **47**, 5–14.

Todd, S.W. (2006). Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. *J. Appl. Ecol.* **43**, 293–304.

Travaini, A., Bustamante, J., Rodríguez, A., Zapata, S., Procopio, D., Pedrana, J. & Martínez Peck, R. (2007). An integrated framework to map animal distributions in large and remote regions. *Divers. Distrib.* **13**, 289–298.

Turner, M.D. & Hiernaux, P. (2002). The use of herders' accounts to map livestock activities across agropastoral landscapes in Semi-Arid Africa. *Landsc. Ecol.* **17**, 367–385.

Wiegand, T., Gunatilleke, S. & Gunatilleke, N. (2007). Species associations in a heterogeneous Sri Lankan dipterocarp forest. *Am. Nat.* **170**, E77–E95.

Wiegand, T., Naves, J., Garbulsky, M.F. & Fernández, N. (2008). Animal habitat quality and ecosystem functioning: exploring seasonal patterns using ndvi. *Ecol. Monogr.* **78**, 87–103.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Can. J. Zool.* **77**, 1223–1232.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Effective sampled area.

Table S1. Coefficients of the final models for *L. guanicoe*, large and small livestock in each seasonal period. References: ps: spring–summer; fw: fall–winter.