CSIRO PUBLISHING
Wildlife Research
https://doi.org/10.1071/WR18085

Environmental factors influencing guanaco distribution and abundance in central Patagonia, Argentina

Julieta Pedrana[A,B,F], *Alejandro Travaini*[A], *Juan Ignacio Zanón*[C], *Sonia Cristina Zapata*[A], *Alejandro Rodríguez*[D] and *Javier Bustamante*[E]

[A]Centro de Investigación Puerto Deseado, Universidad Nacional de la Patagonia Austral, CONICET, Avenida Prefectura Naval S/N, 9050 Puerto Deseado, Santa Cruz, Argentina.
[B]Present address: Recursos Naturales y Gestión Ambiental. Instituto Nacional de Tecnología Agropecuaria, EEA Balcarce, CC 276, 7620 Balcarce, Argentina.
[C]Instituto de Ciencias de la Tierra y Ambientales de La Pampa (INCITAP-CONICET), Universidad Nacional de La Pampa, Avenida Uruguay 151, 6300 Santa Rosa, Argentina.
[D]Department of Conservation Biology. Estación Biológica de Doñana, CSIC, C/Américo Vespucio 26, 41092 Sevilla, España.
[E]Department of Wetland Ecology & Remote Sensing and GIS lab (LAST-EBD), Estación Biológica de Doñana, CSIC, C/Américo Vespucio 26, 41092 Sevilla, España.
[F]Corresponding author. Email: pedrana.julieta@inta.gob.ar

Abstract

Context. The guanaco is the largest wild herbivore inhabiting the Patagonian steppes. Since the end of the 19th Century, it has suffered a progressive decline in numbers owing to poaching and unregulated hunting because of on an assumed competition with sheep. Unfortunately, there has never been a management program for guanaco populations in Argentine Patagonia. Consequently, the guanaco is still considered a pest species by ranchers and has never been considered profitable in the range management model implemented in Patagonia.

Aims. The present article updates the distribution limits of guanaco and estimate its abundance across Chubut, a large province of Patagonia, Argentina. The relative effects of several environmental and anthropogenic factors on guanaco distribution are also assessed.

Methods. Road surveys (7010 km) and species distribution modelling were used to build a habitat suitability model and a distribution map. A distance sampling method was used to estimate guanaco population densities and size. The survey effort required to monitor population trends in this region was also calculated.

Key results. According to the best habitat suitability model, guanaco distribution decreased with altitude and primary productivity, as measured by Normalised Difference Vegetation Index (NDVI), and increased with the distance to the nearest urban centre and oil field. Guanaco distribution showed a clear geographical pattern in Chubut, with low to medium occurrence probability towards the west and higher values towards the east. Guanaco population size was estimated as 657 304 individuals (95% CI 457 437 to 944 059), with a mean density of 2.97 guanacos km^{-2}. Finally, through simulations of guanaco monitoring, it was estimated that an annual survey effort of 10 to thirty 30-km road transects is needed to detect with confidence a significant population decrease or increase over the next 6 or 10 years.

Conclusions. The habitat suitability map presented herein highlights areas with high guanaco densities in Chubut, where it would be possible to identify ranches suitable for performing profitable herding and shearing experiences.

Implications. The maps of guanaco distribution and density, as well as the survey effort required to monitor population trends, may be used to inform decisions concerning the sustainable use of this species.

Additional keywords: habitat models, *Lama guanicoe*, monitoring, predictive cartography, population density.

Received 7 May 2018, accepted 5 October 2018, published online 16 January 2019

Introduction

Patagonian pastoral systems were uniquely based on sheep ranching from the very initial land occupation by European settlers (1880–1930; Soriano and Paruelo 1990). This was followed by the increase and stabilisation of sheep stocks and capital accumulation (1930–80), up to full land occupation. Consequently, the carrying capacity of grasslands progressively began to decrease while steppe degradation increased (Golluscio *et al*. 1998). As a result, there has been a rural depopulation process that started in the 1980s, more evident nowadays in the southern provinces of Argentina (e.g. Santa Cruz and Chubut; Borrelli and Cibils 2005). Throughout these 135 years, wildlife has never been considered as an economically profitable option (e.g. wool, meat, and even tourism) by the government of Argentina, nor a complementary income to domestic livestock production by ranchers (Caro *et al*. 2017). Now, national or regional agricultural guidelines should acknowledge that arid and semiarid Patagonian rangelands cannot be sustainably developed using only conventional meat and wool production systems. Thus, animal production cannot generally be increased, or even sustained, without further degrading the natural capital, i.e. the grasslands. The consequences of overgrazing on the productivity and profitability of rangelands have been found to be severe (Ares *et al*. 1990). In contrast, wildlife might be potentially amenable to community-based sustainable management, which is an increasingly desirable exploitation model (Roth and Merz 1996). This would allow diversification of the local economy that, with the addition of services and marketing, would raise incomes without over-utilising natural capital. This scenario gives wildlife use a comparative advantage in arid rangelands and allows for sustainable economic development (Child 1988). It also provides the opportunity to test the ecological advantages of multi-species systems over traditional livestock production systems based on a single species. In South Africa, for example, there are now 10 000 to 14 000 private ranchers that promote wildlife enterprises alone or in combination with domestic livestock (Child *et al*. 2012). This is an example of an important conservation success that has been accompanied by the improvement of social wellbeing through economic growth and employment creation.

The guanaco (*Lama guanicoe* Müller, 1776) is the largest herbivore of the Patagonian steppe (Redford and Eisenberg 1992) and has an extraordinary potential for a sustainable use (Franklin *et al*. 1997), something that could be enhanced if ranchers and others social actors (e.g. politicians, economists, governors) were aware of the added value of guanaco products such as fibre, leather and meat (Lichtenstein and Carmanchahi 2012). Until recently, guanacos, as well as other wildlife species (e.g. the lesser rhea, *Rhea pennata*), have never been considered economically profitable in the range management model implemented in Argentine Patagonia (Von Thüngen and Lanari 2010). In addition, ranchers from Santa Cruz province categorise the guanaco as a pest species and have a negative attitude towards it (Caro *et al*. 2017). Guanaco wool has a particularly fine fibre that can be obtained through live-shearing of wild individuals (Montes *et al*. 2006; Sacchero *et al*. 2006), using shearing machines that guarantee a residual fibre of appropriate length to avoid excessive heat loss in a cold environment (Gerken 2010). Sheep ranchers from northern Patagonia are gaining expertise at shearing guanacos, which is currently allowed by Argentinean legislation (Baldi *et al*. 2010). Unfortunately, the guanaco is still considered, and consequently treated, as a pest species by ranchers in the southern provinces (Baldi *et al*. 2010; Schroeder *et al*. 2014).

Guanacos are distributed in an extensive range of arid and semiarid habitats, from sea level to 4500 m, from northern Peru to central Chile, and across Argentinean and Chilean Patagonia. Although this species has been considered a highly adaptable camelid with a broad distributional range (Franklin 1983), the guanaco has experienced a progressive drop in numbers and also a parallel reduction of its geographic range (Franklin *et al*. 1997). This decline has been attributed to unregulated hunting and poaching (Franklin 1983; Donadio and Burskik 2006) prompted by an assumed competition with sheep for water and food (Franklin 1983; Pedrana *et al*. 2010). Although the guanaco is not considered a threatened species at the continental level (Baldi *et al*. 2016), some populations could be at risk of disappearing (Wheeler 2006) or may be locally extinct as a result of hunting and habitat loss (Baldi *et al*. 2010). These conservation problems may be relatively local and apparently hardly apply to all of Patagonia (Zanón Martínez *et al*. 2012). In addition, most populations are restricted to low-quality habitats because areas with high primary productivity are occupied by sheep (Pedrana *et al*. 2010).

Any activity based on the guanaco that is economically profitable will generate a more positive perception of guanacos by sheep ranchers (Nabte *et al*. 2013) and less conflict by way of competition for food and water (Baldi *et al*. 2001). The unresolved situation between the guanaco and sheep ranching activities in Argentine Patagonia has led the Santa Cruz Provincial Agricultural Council (CAP) to consider declaring guanacos as a pest and to develop mitigation actions to reduce guanaco populations, such as encouraging indiscriminate hunting across the entire province and to execute culling as part of their management plan (Schroeder *et al*. 2014).

The human–guanaco relationship, including commercial use and conflict in the Patagonian steppes, makes it necessary to update its present distribution and evaluate its abundance, as well as to understand the underlying environmental and anthropogenic drivers on their regional distribution. Thus, this information should be essential to generate detailed knowledge for the sustainability of guanaco exploitation. The aims of the present study were: (1) assessing the relative effects of environmental and anthropogenic factors on guanaco distribution in a large region of Patagonia; (2) generating predictive distribution maps of guanaco at a regional scale, using habitat suitability models; (3) estimating guanaco density and population size for this region; and (4) based on guanaco abundance at the time of the present study, evaluating the sampling effort needed to monitor guanaco populations under two possible scenarios, namely its sustainable exploitation and the unlikely, but not impossible, success in the initiative to declare the species as potentially detrimental for sheep husbandry. We also discuss and compare the results obtained in the present study with those of similar surveys in the adjacent Santa Cruz province (Pedrana *et al*. 2010; Travaini *et al*. 2015).

Materials and methods

Study area

Chubut, with a total area of 224 686 km^2, represents 6% of Argentina and is the second largest Patagonian province (42–46°S, 63–72°W, Fig. 1). This region has a cool-temperate and dry climate with strong and predominantly west winds, and with a mean annual temperature that usually ranges between 6 and 12°C (Paruelo *et al*. 1998). Annual precipitation of ~200 mm (Paruelo *et al*. 1998) concentrates during winter and is strongly influenced by general circulation patterns, the Pacific air masses and the Andes topographic barrier parallel to the Pacific coast, resulting in a strong west–east gradient (Barros *et al*. 1979). The dominant vegetation type is shrub steppe composed of medium height to dwarf shrubs (*Nassauvia glomerulosa*, *N. ulicina*, *Chuquiraga aurea*, *C. avellanedae*) with variable tussock grass cover (*Stipa humilis*, *S. ibari*). Extensive sheep grazing is the predominant agricultural practice in Patagonia. Merino sheep of varying quality are kept in the field throughout the year, herded accordingly to a summer–winter rotation scheme and fed with a varying seasonal forage depending on landscape and altitude (Ares *et al*. 1990). Ecosystem degradation has been attributed to human management factors such as overestimation of carrying capacity of the rangelands, inadequate distribution of animals in extremely large, heterogeneous paddocks and year-long continuous grazing (Golluscio *et al*. 1998).

Study species

Guanacos are sexually monomorphic camelids that aggregate in social groups during the summer breeding season. According to Franklin (1983) and Young and Franklin (2004), the spatial distribution of populations is influenced by a mating system of resource defence polygyny (a territorial system wherein males compete for access to resources required by females). Guanacos can be found in three basic social units: family groups (a male with a group of females and their progeny younger than one-year old, called 'chulengos'), non-reproductive male groups and solitary males. A fourth potential social unit, female groups, was only described during intensive field studies in Torres del Paine National Park, Chile (Ortega and Franklin 1995), but this social unit was not considered in our guanaco censuses because it was uncommon even in the study reporting it (8% of all social units observed, Ortega and Franklin 1995) and might include several females with young, making female groups indistinguishable from family groups. Pedrana *et al*. (2009) empirically demonstrated that only family groups with chulengos can be unequivocally identified during surveys by vehicle, and that the identification of male groups was also challenging because these could be mistaken for family groups without or with undetected chulengos. During the present study we used four observable social units as a form of stratification to produce separate density estimates: breeding groups (family groups with detected chulengos); non-breeding groups (groups without chulengos); solitary animals; and undetermined (groups that could not be clearly assigned to any of the first three categories, Pedrana *et al*. 2009).

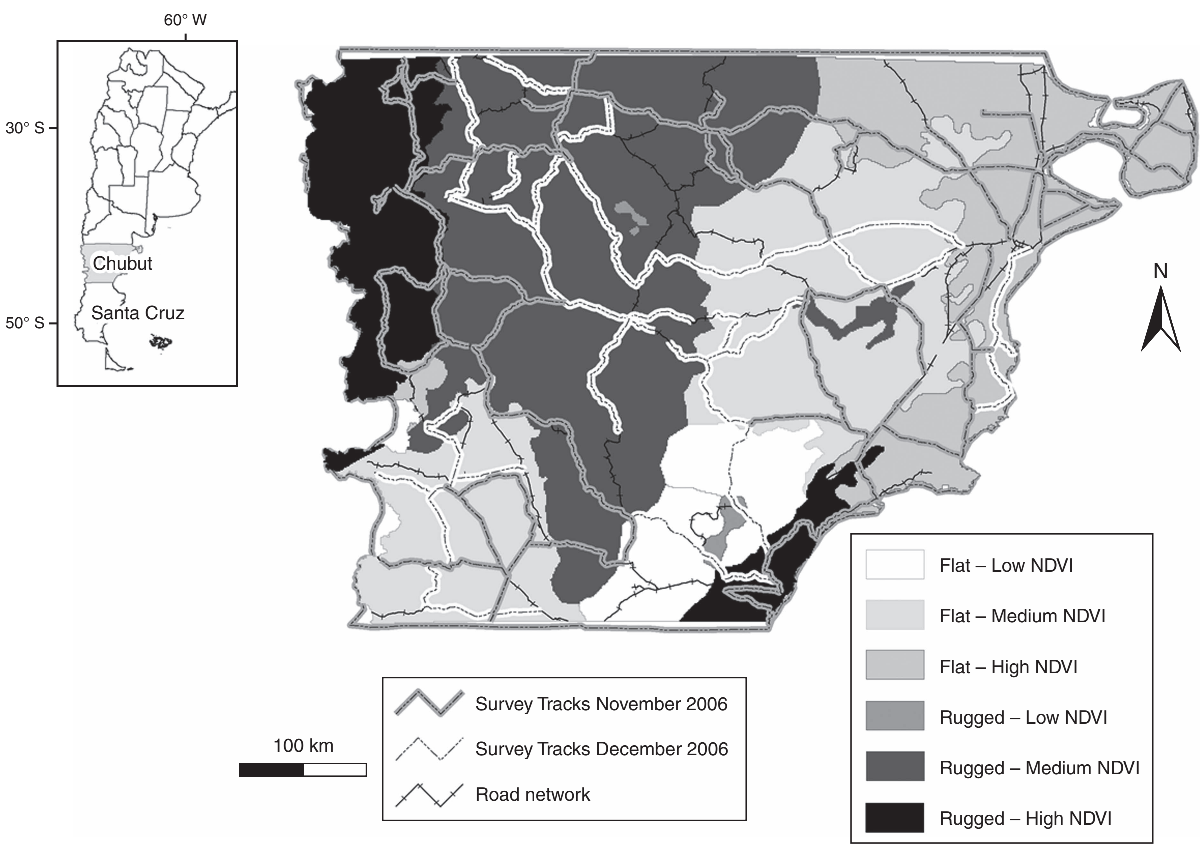

Fig. 1. Study area stratification based on productivity (three Normalised Difference Vegetation Index (NDVI) categories: low, medium and high) and topography (two categories: flat and rugged terrain) and roads surveyed in central Patagonia, Argentina.

Sampling unit selection and field work

To account for the expected regional variation in guanaco densities associated with major environmental variability, we used a stratified random design to select the road segments to be surveyed. For this reason, we categorised the study area into six geographical regions based on the combination of two habitat characteristics that affect guanaco detection and density: (1) Normalised Difference Vegetation Index (NDVI); and (2) mean slope (Fig. 1; Travaini *et al*. 2007). Indeed, both variables influenced guanaco distribution in Santa Cruz (Pedrana *et al*. 2010).

Field work was conducted during one austral spring–summer, which overlaps with guanaco breeding season. Using a vector data of road coverage, we randomly selected 110 survey tracks (road segments of 5 to 80 km) that summed to 4440 km of transects during the first survey (9–27 November 2006, Fig. 1). During our second survey (7–17 December 2006), we randomly selected another 54 survey tracks that added up to 2570 km (Fig. 1). Almost 90% of the survey tracks were dirt and secondary roads with very low traffic density (i.e. fewer than 10 vehicles per day).

Because of their body size, colouration and behaviour, guanacos are easily observable from vehicles driving on roads and secondary trails (Puig 1995) in the open steppe or shrub-steppe. These conditions are excellent for estimating presence and even abundance by vehicle survey using distance sampling methodology (Buckland *et al*. 2001). Road surveys were carried out from a vehicle driving mostly at a speed of 20 km h^{-1} with a driver and one observer during one breeding season (Fig. 1), following recommendations by Pedrana *et al*. (2010). When a guanaco was detected, we stopped the vehicle, recorded group size, and assigned the group to one of our observable social groups. We measured the distance to the animal or the group centre with a laser range finder (Leica LRF 1200 Rangemaster, Germany). We also recorded the azimuth of the observer's trajectory obtained from the inertial compass of a GPS unit (Garmin GPS mapR 76S, USA), and the angle of the animal relative to our bearing (using a protractor). Distance and azimuth allowed us to obtain the actual positions of guanacos and their perpendicular distance to the survey line, as required by distance-sampling methods (Buckland *et al*. 2001). All data were collected in a personal digital assistant (PDA, Tungsten T3, USA) synchronised with the GPS, which was used to record the trajectory and location of the survey track.

Habitat suitability maps for guanaco

We selected eight potential predictors that summarised the most relevant environmental and landscape gradients, as well as anthropogenic features needed to assess which factors might influence the regional distribution of guanacos (Table 1; for further details see Travaini *et al*. 2007; Pedrana *et al*. 2010). Distribution modelling requires defining units in which presence or absence is recorded. For this purpose, we overlaid the surveyed tracks on top of a 1-km grid, following the spatial resolution of NDVI data. Then, the original 457 sightings registered during field surveys were also overlaid and grid cells with at least one guanaco sighting were considered as a presence cell and all remaining cells traversed by census tracks were considered as absences. As cells with guanaco presence ($n = 310$) were outnumbered by absence cells ($n = 15\,606$), we used a resampling scheme to obtain a presence/absence balanced sample (Travaini *et al*. 2015). We randomly selected 310 out of the 15 606 cells with guanaco absences, repeating this procedure 100 times. Each time we generated two datasets: a random sample of 80% of the cells for calibrating the occurrence models; and the remaining 20% for evaluating the models (hereafter referred as the construction and evaluation datasets). All the cells with presence were used in each repetition, while cells with absence were sampled without replacement.

Table 1. Description of the variables used in the predictive distribution models developed for guanaco in central Patagonia Argentina

NVDI, Normalised Difference Vegetation Index

Predictor	Predictor description
Mean.NDVI	Mean Normalised Difference Vegetation Index calculated by using the VGT-S10 product that is a 10-day maximum composite value from the VEGETATION sensor on board of Spot-4 satellite from April 1999 to March 2005.
Season.MAX	Month at which the NDVI reaches its annual maximum value.
CV.NDVI	Coefficient of variation of NDVI.
Distance.stream	Distance (km) to the nearest stream or river.
Altitude	Mean elevation in meters above sea level of the focal cell obtained from the Shuttle Radar Topographic Mission Elevation (SRTM).
Slope	Terrain slope in degrees in a 1 km pixel from the SRTM.
Distance.urban	Distance (km) to the nearest urban area.
Distance.oil	Distance (km) to the nearest oil camp.

To identify which predictors were most likely to affect guanaco occurrence, model fitting was done on the construction dataset with Generalised Additive Models (GAMs, Hastie and Tibshirani 1990) using a binomial error and a logit link. Predictors for the models were selected by a backward–forward stepwise procedure (Sakamoto *et al*. 1986). The Akaike Information Criterion (AIC) was used to retain a term (Burnham and Anderson 2002). We considered as competing models those for which the differences between AIC and the AIC of the best candidate model (the one with the smallest AIC) was $\Delta \leq 2$ (Burnham and Anderson 2002).

Model evaluation was made using the validation dataset by comparing predicted and observed values using a threshold-independent metric, i.e. the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) plot, which was computed for each of the 100 fitted models (Murtaugh 1996). The AUC ranges from 0 (when model discrimination is not better than random) to 1 (perfect discriminatory ability). Predictive models were considered usable if AUC $\geq$ 0.7

Finally, predictions of the resulting distribution models were used to create habitat suitability maps (HSM). Predictions for the entire study area were calculated using R version 3.2.2 (R Development Core Team 2016) and transformed to probability maps using IDRISI Selva GIS software (Clark Labs, Worcester, MA, USA). We categorised and mapped the HSM of guanaco occurrence probability in three classes (low: <0.33, medium: 0.33–0.66 and high: >0.66).

Guanaco density estimation

Line transect data were analysed using the DISTANCE program (version 6.0, Buckland *et al*. 2001; Thomas *et al*. 2010). Estimates of guanaco densities were done by fitting a detection function from the perpendicular distances of guanacos to the survey line (Buckland *et al*. 2001). We pooled distance data across all transects within each HSM class of predicted guanaco occurrence to estimate the detection functions $g(x)$ for each social unit in order to attain the required minimum number of observations (Buckland *et al*. 2001). Although detectability varies among transects, the property of 'pooling robustness' ensures the reliability of the abundance estimates (Buckland *et al*. 2001; Thomas *et al*. 2010). Pooling also helps to even out minor fluctuations in object density across surveyed strips and to even out chance fluctuations in object distribution (Fewster *et al*. 2005). The DISTANCE program allows for careful data exploration, facilitating the identification of any outlying observation at extreme distances, or sighting clumping, and suggests appropriate levels of truncation and grouping for detection function fitting. We used the smallest value of AIC to choose the best competing model (Key function + adjustment terms). Density estimates were calculated for each social unit and for all guanaco contacts pooled together, and for each HSM category and for all of Chubut. Considering the extent of each HSM category, density estimates were converted into estimates of population size.

Monitoring program

We estimated and simulated the sampling effort, in terms of number of 30 km transects of road survey, needed to monitor guanaco population in Chubut and also to detect declines from present status in guanaco population using MONITOR (version 11.0.0, Gibbs and Ene 2010). We modelled the encounter rate, which was calculated as the number of guanacos detected per sampled kilometre, over time and to generate detection rates derived from route-regression analyses (Gibbs and Melvin 1997). This simulation procedure is useful for evaluating the trade-offs between sampling effort, logistical constraints and power to detect trends (Field *et al*. 2005). To estimate power we supplied the program with initial estimates of encounter rates and its variance, derived empirically from our own results. We arbitrarily selected 30 km as the length of sampling units. Based on our experience, a 30-km-long transect usually takes about two hours to complete, the interval we used to exchange observers during field work to guarantee observer attention. Additionally, in the study area, random 30-km transects can be selected from the vector data of road coverage more easily than longer segments. To select suitable sampling efforts, we fixed the minimum acceptable power at $(1\text{-}\beta) = 0.80$ (Di Stefano 2001), i.e. the highest probability of failing to detect a real trend was 0.20. Type I error was fixed at 0.05. To define the effect size component, we selected two alternative scenarios, both highly probable given the guanaco current situation previously described. The first scenario is under the hypothesis of a sustainable use of guanaco populations to detect early a 40% decrease in the next six to 10 years. An alternative scenario, the second, is if the guanaco is considered as a pest species in order to early detect a 40% increase in the next six and 10 years. As we had sampled each one of the 164 survey tracks once, random resampling without replacement of 30-km transects was used to estimate the mean and the standard deviation of guanaco encounter rates, as a surrogate of spatial variability. As an estimate of power variability, we estimated the standard deviation from 20 simulations for each monitoring scenario and 2000 iterations for each simulation.

Results

We surveyed 7010 km, almost 76% of available national and provincial roads in Chubut. We recorded 456 guanaco social groups, which added up to 2893 individuals (Table 2). Almost 20% of individuals were registered as belonging to breeding groups, 30% as non-breeding groups and 4% as solitary individuals (Table 2). The remaining 47% of individuals were classified as undetermined (Table 2). The high percentage of undetermined individuals resulted from our interest in minimising the chances of social group misclassification. We opted for considering family groups without juveniles, or with undetected juveniles, as undetermined rather than misclassifying them as non-breeding family groups (Pedrana *et al*. 2009). Family groups (n) averaged 8 (s.d. 3.22) individuals, where the mean number of females and chulengos per group were 5 (s.d. 2.68) and 2 (s.d. 1.17), respectively (Table 2). Non-breeding and undetermined groups averaged 28 (s.d. 15.81) and 6 (s.d. 2.68) individuals per group, respectively (Table 2).

Habitat suitability maps for guanaco

The most parsimonious GAM of guanaco presence incorporated as predictors the mean NDVI, altitude, the distance to the nearest urban centre and to the closest oil field (Table S1, available

Table 2. Number of guanaco groups and individuals (within brackets) and mean group size recorded during one breeding season (November–December 2006) in the three areas defined by Habitat Suitability Maps (HSM) and for the total area covered in central Patagonia, Argentina

s.d., standard deviation; Und., Undetermined groups

HSM classes	Area (km^2)	Effort (km) (# transects)	Guanaco social groups (individuals) Solitary	Breeding	Non Breeding	Und.	Total	Mean group size (s.d.) Breeding	*Females per group*	*Chulengos per group*	Non Breeding	Und.
Low	76 741	1824 (46)	14	6 (42)	5 (159)	13 (91)	38 (306)	7 (3.00)	5 (2.89)	1 (1.03)	32 (22.72)	7 (4.38)
Medium	68 145	3686 (82)	46	26 (216)	16 (444)	120 (710)	208 (1416)	8 (3.31)	5 (2.83)	2 (1.27)	28 (14.3)	6 (4.27)
High	76 205	1500 (36)	65	35 (294)	10 (259)	100 (553)	210 (1171)	8 (3.25)	6 (2.58)	2 (1.21)	16 (25.90)	6 (3.59)
Total	221 091	7010 (164)	125	67 (552)	31 (862)	233 (1354)	456 (2893)	8 (3.22)	5 (2.68)	2 (1.17)	28 (15.81)	6 (2.68)

as Supplementary Material to this paper). The probability of guanaco occurrence decreased with primary productivity and with mean altitude, whereas it increased with the distance to the nearest urban centre and oil field (Fig. 2).

The mean (± s.e.) AUC of the best model ranged from 0.80 (±0.02) to 0.82 (±0.02) for the evaluation dataset (Table S1). These results indicate that models have an acceptable discrimination ability and are useful for predicting guanaco distribution.

The HSM of guanaco occurrence (Fig. 3), corresponding to the predictions of the best model (Table S1), showed that the probability of guanaco occurrence was positively associated with a gradient of increasing aridity from west to east. Areas with low probability of guanaco occurrence predominated throughout the western third of Chubut, within the sub-Andean and occidental physiographic districts (Soriano 1956), from the transition from forests to short grasslands steppes and scrublands to the centre of the Province (Ares *et al.* 1990). From there, the probability of guanaco occurrence steeply increased, eastward up to the coastline and the Valdés Peninsula, throughout the driest lands with the most xeromorphic floristic composition (Fig. 3).

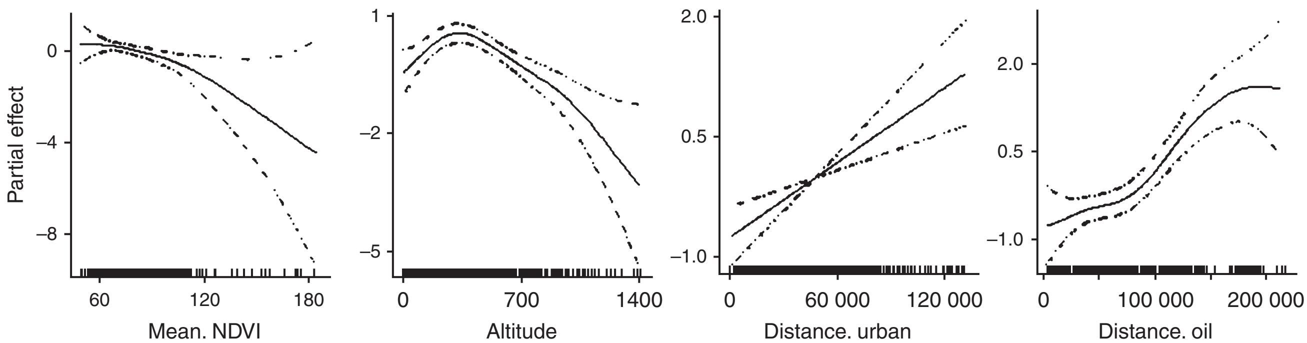

Fig. 2. Partial effects of the predictors included in the most-parsimonious model about the variables influencing guanaco occurrence (Table S1). Dashed lines represent 95% confidence intervals for the mean effect. NDVI, Normalised Difference Vegetation Index.

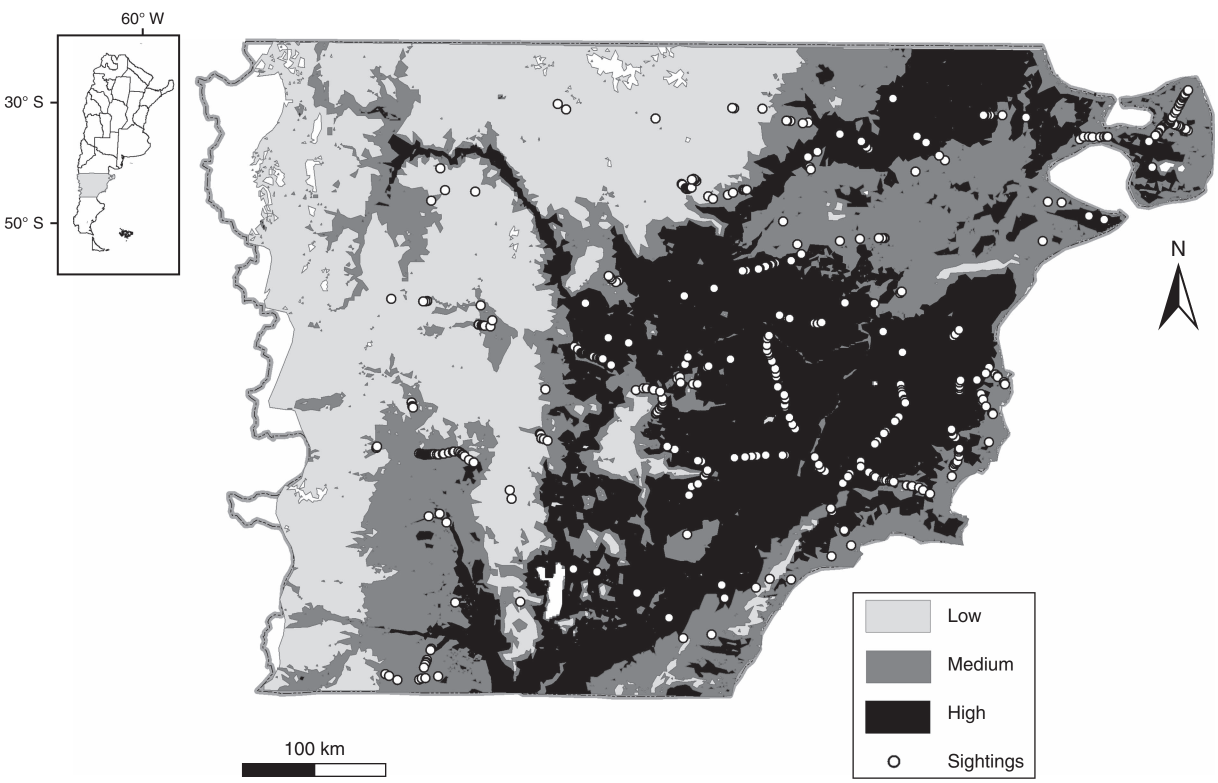

Fig. 3. Habitat suitability map of guanaco constructed from the most parsimonious model (Table S1), in central Patagonia, Argentina. Values represent the probability of guanaco contact in a 1-km cell and are categorised into three classes (low: <0.33, medium: 0.33–0.66, high: >0.66). Guanaco sightings are indicated by circles. Areas in white correspond to regions without predictions: sea, lakes, forested areas or outside the model's environmental space.

Table 3. Estimates of guanaco density (D) and total population size (*N*) for each social group and in each class of Habitat Suitability Map (HSM) in central Patagonia Argentina

Upper and lower limits of 95% confidence of intervals for density estimates are given. CV, coefficient of variation of density estimates

		Group km^{-2}	D (ind km^{-2})	Lower limit	Upper limit	CV	*N*
Social Groups	Breeding	0.08	0.48	0.23	0.98	38.34	105 239
	Non Breeding	0.04	0.21	0.11	0.37	30.71	45 324
	Solitary	0.15	0.85	0.46	1.57	31.94	187 706
	Undetermined	0.25	1.44	0.88	2.36	25.47	318 813
	Pooled	0.51	2.97	2.70	4.27	18.61	657 082
HSM classes	Low	0.09	0.49	0.22	1.10	41.02	38 217
	Medium	0.47	2.74	1.65	4.56	26.22	186 649
	High	0.68	3.93	2.65	5.82	20.16	299 105
	Pooled	0.46	2.69	1.92	3.77	17.36	523 971

Guanaco density estimation

Predictions of guanaco occurrence were not made for water bodies, forests and other habitats unsuitable for guanaco, so the total area for which abundance was estimated included 221 091 km^2, which represents 98% of the extent of Chubut.

After considering competing detection functions, the smallest AIC value indicated that the hazard-rate key, with three-parameter cosine adjustment term should be selected for abundance estimation for each guanaco social group, and one-parameter cosine adjustment term for abundance estimation at each HSM category of guanaco occurrence. We truncated distance data at 200 m in all models, in order to attain a robust line transect analysis after the elimination of outliers (Buckland *et al*. 2001). Our truncation distance closely follows $g(x) = 0.15$, where g is the detection function and x is the perpendicular distance.

For the entire Chubut, we estimated a total guanaco population of 657 082 individuals (95% CI 457 437 to 944 059), which represents a mean density of 2.97 individuals per km^2 (Table 3). Mean density varied considerably between guanaco breeding groups and non-breeding groups, (0.48 and 0.21 individuals per km^2, respectively; Table 3). In areas classified as having low habitat suitability (HS) for guanaco, the estimated density was 0.49 individuals per km^2, whereas in the medium and high HS categories, densities were 2.74 and 3.93 individuals per km^2, respectively. The CV varied between 41 and 20% (Table 3). As expected, mean density positively increased in relation to the HS categories (Table 3).

Guanaco monitoring

Assuming annual monitoring surveys, simulations showed that at least thirty 30-km transects are needed to detect confidently any decrease (sustainable use scenario) or increase (alternative scenario) over the next 6 or 10 years in the low HS category (Fig. 4*a*). Required power (0.80) was attained for most scenarios and HS categories based on a quite reasonable sampling effort. However, power over 0.90 was attained only with 10 30-km transects for any monitoring scenario for the medium and high HS categories (Fig. 4*b*, *c*).

Discussion

The sustainable use of any wildlife species requires a thorough knowledge of its distribution and abundance. Also, it is important to develop a scientifically sound monitoring protocol to evaluate population trends under management. Here, we provide these three elements for the guanaco, a valuable wildlife species that inhabits one of the Neotropical ecosystems most severely affected by desertification.

Guanaco distribution in Chubut showed a clear geographical pattern, with a gradient from low occurrence probability in the west and to higher values in the east (Fig. 3). The areas with higher habitat suitability for the guanaco are coincident with the Patagonian semi-deserts (Paruelo *et al*. 1998) and the Central District' delimited by Soriano (1956) and described by León *et al*. (1998). This is the less productive area in Chubut, although it could be considered one of the most productive semi-deserts (450 kg ha^{-1} year^{-1}) in the world (Paruelo *et al*. 1998). The guanaco distribution pattern observed here has a certain similarity to those described for Tierra del Fuego (Raedeke 1979, 1982) and Santa Cruz (Pedrana *et al*. 2010) provinces, where higher habitat suitability for the species was found in the less productive and more arid areas, in remarkable coincidence with those areas where sheep husbandry is absent or sheep occur at a very low density (Pedrana *et al*. 2010). The west of Chubut, where guanaco density is low, is characterised by a mosaic of shrub-grass steppes with an annual net primary productivity higher than that of the eastern semi-deserts (650 kg ha^{-1} year^{-1} Paruelo *et al*. 1998). Habitat suitability models highlighted the western region as a low-quality habitat for guanaco. Throughout this area, the higher productivity has favoured more intense and sustained sheep ranching (Baldi *et al*. 2001). Probably as a consequence of interference from this activity, guanacos have become scarce, although they seem to have remained in sheep-free less productive areas. Guanaco occurrence in Chubut was positively associated with low productivity areas, characterised by low NDVI values and low elevation, and far away from oil exploitation and urban areas. Our results can be interpreted as a guanaco preference induced by anthropogenic factors for this arid habitat; however, it also seems plausible that this pattern may not reflect a true habitat preference but an indirect response to exogenous factors (competition with sheep and a response to direct persecution by ranchers or poaching). We also found a positive association of guanaco with remote areas, far away from centres of human influence such as cities and oil camps, which is consistent with a guanaco avoidance of areas that could have intensive poaching. These relationships could suggest the hypothesis that

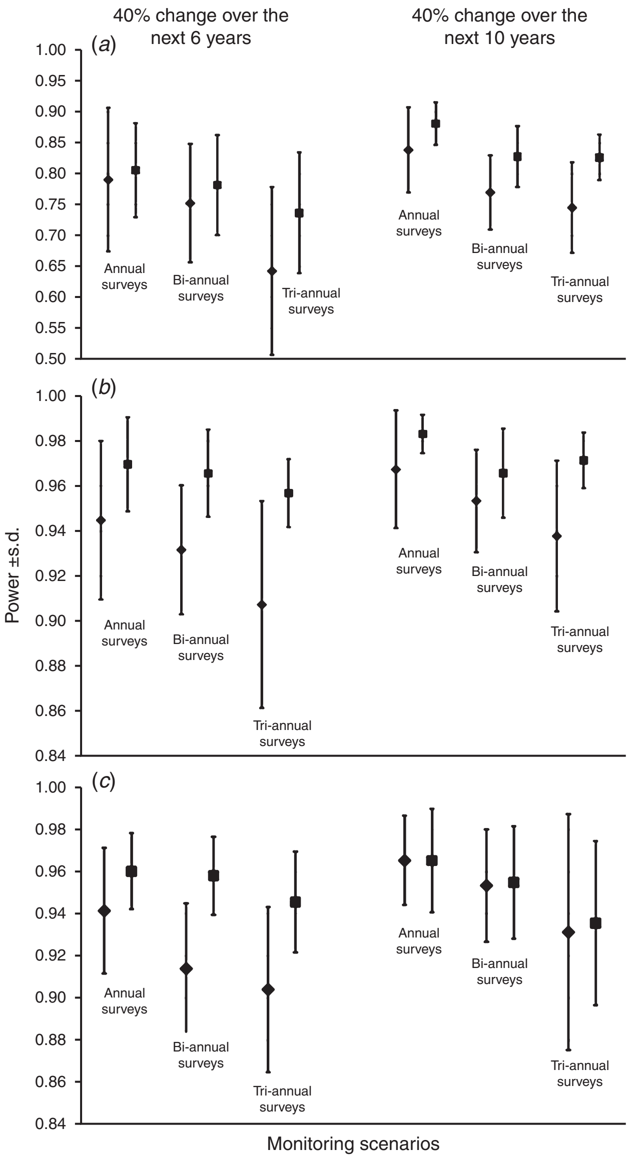

Fig. 4. Power (s.d.) for the detection of a decrease in the Chubut guanaco population (solid diamonds) or an increase (solid squares) under different scenarios, 40% change over the next 6 or 10 years, and survey frequency: (*a*) low-density strata and thirty 30-km transects of road survey; (*b*) medium-density and 10 30-km transects of road survey; and (*c*) high-density strata and 10 30-km transects of road survey.

human activities have a direct and negative effect on guanaco occurrence, suggesting either a behavioural avoidance of sites where mortality risk by humans is high and recurrent, or a true decline of guanaco local population due to overhunting. According to Pedrana *et al*. (2010), the same habitat selection pattern was found in Santa Cruz where high-suitability habitat for guanacos corresponded with the less productive areas.

The extent to which the strong inverse correlation between vegetation productivity and guanaco density depends on avoidance by guanacos of high sheep density areas, their illegal culling by ranchers, or because they actively select more arid vegetation communities remains an unresolved question (Pedrana *et al*. 2010). One way to address this question is estimating guanaco density and modelling habitat in protected areas with different vegetation communities where sheep and poaching has been excluded (or reduced). Comparing guanaco population and density estimates between Chubut and other published guanaco figures is challenging since stratification of the study area, survey effort and estimation methods are quite different. It has been debated that road transects are not an adequate tool for estimating guanaco population size and occurrence (Schroeder *et al*. 2018) because roads rarely cross a region in a random pattern and because guanacos could be attracted or repelled by roads. In Patagonia, besides vehicle survey, there are two alternative methods that could be used to calculate guanaco abundance, but it is unclear that these methods would allow extensive distance sampling over large regions. In the case of horseback, distance sampling has several disadvantages: rugged terrain could hardly be sampled; surveying areas far away from human habitation would be unfeasible (with the consequent bias); and it would be difficult to cover large regions during a short session. Aircraft distance sampling could solve some of these problems but has its own unique disadvantages, such as unreliable counting of individuals or determination of social units. Although sampling away from roads would be desirable, what we propose here is a cost-effective method of density estimation, because aerial surveys are much more expensive than road surveys (Travaini *et al*. 2007) and hence rarely undertaken in practice. Indeed, no published guanaco population estimates exist for large areas based on aerial surveys. We covered three times more distance than the total length of aerial transects reported by Amaya *et al*. (2001). Testing empirically which of the two methods gives more accurate and cost-effective estimates for guanaco density and population size in large areas is an important topic to be addressed in future studies.

According to the International Union for Conservation of Nature (IUCN), most of the world's remaining guanacos occur in Argentina. Argentina is estimated to be home to 1.2–1.9 million guanacos (between 81–86% of the entire population), most of them concentrated in the Patagonian region (Baldi *et al*. 2016). Even though its distribution range is extended in almost all of Argentine Patagonia, guanaco populations seem to be more fragmented in the northern and central provinces (Chubut, Río Negro and Neuquén) compared with the southern ones (Santa Cruz and Tierra del Fuego, Baldi *et al*. 2016). Guanaco local density estimations for Patagonia ranged from 0.40 individuals per km^2 in some areas of Tierra del Fuego (Montes *et al*. 2000), to more than 10 individuals per km^2 in Neuquén (Rey *et al*. 2009), Río Negro (Rey 2010) and Chubut (Saba and Battro 1987). Our guanaco density estimates can be compared with those in Santa Cruz, which were produced using the same methods (Pedrana *et al*. 2010; Travaini *et al*. 2015). In the present study, we found that guanaco densities in Chubut (2–4 individuals per km^2) were lower than those estimated in Santa Cruz (3–7 individuals per km^2, table 2 in Travaini *et al*. 2015). While both provinces are similar in size (Chubut: 221 866 km^2, Santa Cruz: 223 117 km^2), we estimate that the Chubut guanaco population is only half of that in Santa Cruz (Travaini *et al*. 2015).

Finally, if guanaco populations are to be sustained, adaptive management would require the monitoring of these populations for the early detection of any increase or unwanted decrease in their numbers. Traveling 600 km every 3 years is adequate to detect quite large changes within the two most dense guanaco strata in Chubut, where any extractive enterprise might start. Based on our experience, 30-km transects should be distributed throughout the strata area, which we estimate would take six complete working days by two or three technicians (Travaini *et al*. 2015). However, if the low HS category is included in the follow-up, the effort needed would be greater, about nine full-time working days per year, and 15 fieldwork days every 3 years. Ideally, an articulated association between Chubut and its neighbouring Santa Cruz could result in the best benefits both for the monitoring and conservation of guanaco wild populations. Moreover, these two provinces should even develop common strategies for the sustainable use and regulation in the trade of guanaco products.

Conservation and management implications

Patagonia holds some 700 000 km^2 of grasslands and scrublands that still maintain healthy guanaco populations (Baldi *et al*. 2010), despite having been deeply modified by human activities. Both ecosystem structure and functioning were altered by the introduction of domestic herbivores at the beginning of the 20th Century (Aguiar *et al*. 1996; Bisigato and Bertiller 1997). Grazing, mining (Radovani *et al*. 2014) and, more recently, global climate change (Pinto *et al*. 2008) are human-related disturbances acting at different spatial and temporal scales that have degraded Patagonian vegetation. Current conditions are very different from the ones encountered by the first European settlers, who were unable to maintain a traditional sheep ranching system that was environmentally sustainable and economically profitable (Texeira and Paruelo 2006). Traditional sheep ranching involved keeping sheep grazing in extensive paddocks (requiring several thousand hectares), with limited attention a few occasions a year for deworming or shearing (García Brea *et al*. 2010). Restoring the Patagonian shrub-steppe as an ecologically functional ecosystem (Chardonnet *et al*. 2002) would benefit from efficient and modernised sheep husbandry complemented by activities such as the sustainable use of wildlife and ecotourism. In this framework, guanaco could play a role as an important economic resource for landowners and local communities (Franklin *et al*. 1997). In the absence of alternatives, economic incentives could be the most effective driver for the conservation of the species (Fritz and Franklin 1994).

The greatest utility of our results is that they provide an excellent overview of guanaco distribution and abundance in 2006, and the big picture for the entire Chubut, from which the government could start planning the sustainable use of the species. Considering our HSM, it is possible to identify the areas of the territory with higher densities, where it will be easier to select ranches with adequate guanaco abundance (Baldi *et al*. 2010) to develop profitable herding and shearing experiences. Our HSM for Chubut, together with other environmental and human spatial data (e.g. land use, road cover and cadastral), should be used to generate a decision tool that guarantees informed sustainable use of the species. Finally, our results need to be implemented in accordance with environmental education programs to change the perception of ranchers in Chubut province on native wildlife.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This work was primarily funded by the BBVA Foundation through a grant under the Conservation Biology Program to A. Rodríguez, and also by the Agencia Nacional de Promoción Científica y Tecnológica (PICTO N° 30723). Additional support was provided by Universidad Nacional de la Patagonia Austral, CONICET (PEI-6065), and CONAE.

References

Aguiar, M. R., Paruelo, J. M., Sala, O. E., and Laurenroth, W. K. (1996). Ecosystem consequences of plant functional types changes in semiarid grassland. *Journal of Vegetation Science* **7**, 381–390. doi:10.2307/3236281

Amaya, J.N., von Thüngen J., and de Lamo, D.A. (2001). Relevamiento y distribución de guanacos en la Patagonia. Comunicación Técnica no. 109. (Instituto Nacional de Tecnología Agropecuaria: Bariloche, Argentina.) [In Spanish]

Ares, J. O., Beeskow, A. M., Bertiller, M. B., Rostagno, C. M., Irisarri, M. P., Anchorena, J., Defossé, G. E., and Meroni, C. (1990). Structural and dynamic characteristics of overgrazed grasslands of northern Patagonia, Argentina. In 'Managed Grasslands: Regional Studies'. (Ed. A. Breymeyer.) pp. 149–175. (Elsevier: Amsterdam.)

Baldi, R., Albon, S. D., and Elston, D. A. (2001). Guanacos and sheep: evidence for continuing competition in arid Patagonia. *Oecologia* **129**, 561–570. doi:10.1007/s004420100770

Baldi, R., Novaro, A., Funes, M., Walker, S., Ferrando, P., Failla, M., and Carmanchahi, P. (2010). Guanaco management in Patagonian rangelands: a conservation opportunity on the brink of collapse. In 'Conserving Wildlife while Maintaining Livestock in Semi-Arid Ecosystems'. (Eds J. Du Toit, R. Kock and J. Deutsch.) pp. 266–290. (Blackwell Publishing: Oxford, UK.)

Baldi, R., Acebes, P., Cuéllar, E., Funes, M., Hoces, D., Puig, S., and Franklin, W. L. (2016). *Lama guanicoe*. The IUCN Red List of Threatened Species 2016. Available at http://www.iucnredlist.org [Accessed 6 April 2018]

Barros, V. R., Scian, B. V., and Mattio, H. F. (1979). Campos de precipitación de la provincia de Chubut (1931–1960). *Geoacta* **10**, 175–192.

Bisigato, A. J., and Bertiller, M. B. (1997). Grazing effects on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments* **36**, 639–653. doi:10.1006/jare.1996.0247

Borrelli, P., and Cibils, A. (2005). Rural depopulation and grassland management in Patagonia. In 'Grasslands: Development, Opportunities, Perspectives'. (Eds S. G. Reynolds and J. Frame.) pp. 461–488. (FAO: Enfield, NH.)

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). 'Introduction to Distance Sampling: Estimating Abundance of Biological Populations.' (Oxford University Press: Oxford.)

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: a Practical Information-theoretic Approach.' (Springer-Verlag: New York.)

Caro, J., Zapata, S. C., Zanón, J. I., Rodríguez, A., and Travaini, A. (2017). Ganadería ovina y usos alternativos del suelo en la Patagonia austral, Argentina. *Multequina (Mendoza)* **26**, 33–50.

Chardonnet, P., des Clers, B., Fischer, J., Gerhold, R., Jori, F., and Lamarque, F. (2002). The value of wildlife. *Revue scientifique et technique (International Office of Epizootics)* **21**, 15–51.

Child, B. A. (1988). The economic potential and utilization of wildlife in Zimbabwe. *Revue scientifique et technique (International Office of Epizootics)* **7**, 773–782.

Child, B. A., Musengezi, J., Parent, G. D., and Child, G. F. T. (2012). The economics and institutional economics of wildlife on private land in Africa. *Pastoralism* **2**, 18. doi:10.1186/2041-7136-2-18

Di Stefano, J. (2001). Power analysis and sustainable forest management. *Forest Ecology and Management* **154**, 141–153. doi:10.1016/S0378-1127(00)00627-7

Donadio, E., and Burskik, S. W. (2006). Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biological Conservation* **127**, 139–145. doi:10.1016/j.biocon.2005.08.004

Fewster, R. M., Laake, J. L., and Buckland, S. T. (2005). Line transect sampling in small and large regions. *Biometrics* **61**, 856–861. doi:10.1111/j.1541-0420.2005.00413_1.x

Field, S. A., Tyre, A. J., and Possingham, H. P. (2005). Optimizing allocation of monitoring effort under economic and observational constraints. *The Journal of Wildlife Management* **69**, 473–482. doi:10.2193/0022-541X(2005)069[0473:OAOMEU]2.0.CO;2

Franklin, W. L. (1983). Contrasting socioecologies of South America's camelids: the vicugna and Guanaco. In 'Advances in the Study of Mammalian Behavior'. (Eds J. F. Eisenberg and D. Kleiman.) pp. 573–629. (Special Publications No. 7, American Society of Mammalogists: Shippensburg, PA.)

Franklin, W. L., Bas, F., Bonacic, C. F., Cunazza, C., and Soto, N. (1997). Striving to manage Patagonia guanacos for sustained use in the grazing agroecosystem of southern Chile. *Wildlife Society Bulletin* **25**, 65–73.

Fritz, M. A., and Franklin, W. L. (1994). First estimates of guanaco male group harvestability in the Patagonia of South America. *Vida Silvestre Neotropical* **3**, 84–90.

García Brea, A., Zapata, S. C., Procopio, D. E., Martínez Peck, R., and Travaini, A. (2010). Evaluación del interés de productores ganaderos en el control selectivo y eficiente de predadores en la Patagonia Austral. *Acta Zoológica Mexicana* **26**, 303–321. doi:10.21829/azm.2010.262703

Gerken, M. (2010). Relationships between integumental characteristics and thermoregulation in South American camelids. *Animal* **4**, 1451–1459. doi:10.1017/S1751731109991443

Gibbs, J. P., and Ene, E. (2010). Program monitor: estimating the statistical power of ecological monitoring programs. Version 11.0.0. Available at http://www.esf.edu/efb/gibbs/monitor [Accessed 9 April 2018]

Gibbs, J. P., and Melvin, S. M. (1997). Power to detect trends in waterbird abundance with call–response surveys. *The Journal of Wildlife Management* **61**, 1262–1267. doi:10.2307/3802125

Golluscio, R. A., Deregibus, V. A., and Paruelo, J. M. (1998). Sustainability and range management in the Patagonian steppes. *Ecología Austral* **8**, 265–284.

Hastie, T. J., and Tibshirani, R. J. (1990). 'Generalized Additive Models.' (Chapman & Hall: London.)

León, R. J. C., Bran, D., Collantes, M., Paruelo, J. M., and Soriano, A. (1998). Grandes unidades de vegetación en la Patagonia. *Ecología Austral* **8**, 123–141.

Lichtenstein, G., and Carmanchahi, P. D. (2012). Guanaco management by pastoralists in the Southern Andes. *Pastoralism* **2**, 1–16. doi:10.1186/2041-7136-2-16

Montes, C., De Lamo, D. A., and Zavatti, J. (2000). Distribución de abundancias de Guanacos (*Lama guanicoe*) en los distintos ambientes de Tierra del Fuego, Argentina. *Mastozoología Neotropical* **7**, 23–31.

Montes, M. C., Carmanchahi, P. D., Rey, A., and Funes, M. (2006). Live shearing free-ranging guanacos (*Lama guanicoe*) in Patagonia for sustainable use. *Journal of Arid Environments* **64**, 616–625. doi:10.1016/j.jaridenv.2005.05.008

Murtaugh, P. A. (1996). The statistical evaluation of ecological indicators. *Ecological Applications* **6**, 132–139. doi:10.2307/2269559

Nabte, M. J., Marino, A. I., Rodríguez, M. V., Monjeau, A., and Saba, S. L. (2013). Range management affects native ungulate populations in Peninsula Valdés, a World Natural Heritage. *PLoS One* **8**, e55655. doi:10.1371/journal.pone.0055655

Ortega, I. M., and Franklin, W. I. (1995). Social organization, distribution and movements of a migratory Guanaco population in the Chilean Patagonia. *Revista Chilena de Historia Natural* **68**, 489–500.

Paruelo, J. M., Jobbágy, E. G., and Sala, O. E. (1998). Biozones of Patagonia. *Ecología Austral* **8**, 145–153.

Pedrana, J., Rodríguez, A., Bustamante, J., Travaini, A., and Zanón Martínez, J. I. (2009). Failure to estimate reliable sex ratios of guanaco from road-survey data. *Canadian Journal of Zoology* **87**, 886–894. doi:10.1139/Z09-079

Pedrana, J., Bustamante, J., Travaini, A., and Rodríguez, A. (2010). Factors influencing guanaco distribution in southern Argentine Patagonia and implications for its sustainable use. *Biodiversity and Conservation* **19**, 3499–3512. doi:10.1007/s10531-010-9910-1

Pinto, J., Bonacic, C., Hamilton-West, C., Romero, J., and Lubroth, J. (2008). Climate change and animal diseases in South America. *International Office of Epizootics* **27**, 599–613.

Puig, S. (1995). Abundancia y distribución de las poblaciones de Guanacos. In 'Técnicas para el manejo del Guanaco'. (Ed. S. Puig.) pp. 57–68. (IUCN: Gland, Switzerland.) [In Spanish]

R Development Core Team (2016). 'R: A Language and Environment for Statistical Computing.' Available at www.R-project.org [Verified 11 November 2018]

Radovani, N. I., Funes, M. C., Walker, R. S., Gader, R., and Novaro, A. J. (2014). Guanaco *Lama guanicoe* numbers plummet in an area subject to poaching from oil-exploration trails in Patagonia. *Oryx* **49**, 1–9.

Raedeke, K. H. (1979). Population dynamics and socioecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. Ph.D. Thesis, University of Washington, Seattle, WA.

Raedeke, K. H. (1982). Habitat use by guanacos (*Lama guanicoe*) and sheep on common range, Tierra del Fuego, Chile. *Turrialba* **32**, 309–314.

Redford, K. H., and Eisenberg, J. F. (1992). 'Mammals of the Neotropics: the Southern Cone.' (The University of Chicago Press: Chicago, IL.)

Rey, A. (2010). Efectos del manejo sobre la dinámica de poblaciones de guanacos silvestres (*Lama guanicoe*) y mortalidad por enganches en alambrados en campos ganaderos de Patagonia Norte, Argentina. Ph.D. Thesis, University of Buenos Aires, Argentina. [In Spanish]

Rey, A., Carmanchahi, P. D., Puig, S., and Guichón, M. L. (2009). Densidad, estructura social, actividad y manejo de guanacos silvestres (*Lama guanicoe*) en el sur del Neuquén, Argentina. *Mastozoología Neotropical* **16**, 389–401.

Roth, H. H., and Merz, G. (1996). 'Wildlife Resources, a Global Account of Economic Use.' (Springer: Berlin.)

Saba, S. L., and Battro, P. (1987). Estimación de la densidad poblacional de Guanacos (*Lama guanicoe* Muller). *Turrialba* **37**, 113–118.

Sacchero, D., Maurino, M. J., and Lanari, M. R. (2006). Diferencias de calidad y proporción de down en muestras individuales de vellones de Guanaco (*Lama guanicoe*) en distintas ecorregiones de Argentina. *Revista Argentina de Producción Animal* **26**, 211–216.

Sakamoto, Y., Ishiguro, M., and Kitagawa, G. (1986). 'Akaike information criterion statistics.' (KTK Scientific Publishers: Tokyo.)

Schroeder, N., Matteucci, S. D., Moreno, P. G., Gregorio, P., Ovejero, R., Taraborelli, P., and Carmanchahi, P. D. (2014). Spatial and seasonal dynamic of abundance and distribution of guanaco and livestock: insights from using density surface and null models. *PLoS One* **9**, e85960. doi:10.1371/journal.pone.0085960

Schroeder, N. M., González, A., Wisdom, M., Nielson, R., Rowland, M. M., and Novaro, A. J. (2018). Roads have no effect on guanaco habitat selection at a Patagonian site with limited poaching. *Global Ecology and Conservation* **14**, e00394. doi:10.1016/j.gecco.2018.e00394

Soriano, A. (1956). Los distritos florísticos de la Provincia Patagónica. *Revista Investigación Agropecuaria* **10**, 323–347.

Soriano, A., and Paruelo, J. M. (1990). El manejo de campos de pastoreo en Patagonia: aplicación de principios ecológicos. *Ciencia Hoy* **2**, 44–53.

Texeira, M., and Paruelo, J. M. (2006). Demography, population dynamics and sustainability of the Patagonian sheep flocks. *Agricultural Systems* **87**, 123–146. doi:10.1016/j.agsy.2004.11.005

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., and Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**, 5–14. doi:10.1111/j.1365-2664.2009.01737.x

Travaini, A., Bustamante, J., Rodríguez, A., Zapata, S., Procopio, D., Pedrana, J., and Martínez Peck, R. (2007). An integrated framework to map animal distributions in large and remote regions. *Diversity & Distributions* **13**, 289–298. doi:10.1111/j.1472-4642.2007.00338.x

Travaini, A., Zapata, S. C., Bustamante, J., Pedrana, J., Zanón, J. I., and Rodríguez, A. (2015). Guanaco abundance and monitoring in Southern Patagonia: distance sampling reveals substantially greater numbers than previously reported. *Zoological Studies (Taipei, Taiwan)* **54**, 23.

Von Thüngen, J., and Lanari, M. R. (2010). Profitability of sheep farming and wildlife management in Patagonia. *Pastoralism* **1**, 274–290.

Wheeler, J. C. (2006). Guanaco 1: Working to save Peru's endangered guanacos. *Camelid Quiarterly* **5**, 39–42.

Young, J. K., and Franklin, W. L. (2004). Territorial fidelity of male guanacos in the Patagonia of Southern Chile. *Journal of Mammalogy* **85**, 72–78. doi:10.1644/1545-1542(2004)085<0072:TFOMGI>2.0.CO;2

Zanón Martínez, J. I., Travaini, A., Zapata, S. C., Procopio, D., and Santillán, M. A. (2012). The ecological role of native and introduced species in the diet of the puma *Puma concolor* in southern Patagonia. *Oryx* **46**, 106–111. doi:10.1017/S0030605310001821