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Diffusive dispersal in a growing ungulate population: guanaco expansion beyond the limits of protected areas

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Abstract Growth of wild ungulate populations within protected areas can cause an expansion towards surrounding non-protected areas and lead to conflicts with human activities. The spatial and demographic structure of colonizing populations inform about their state and potential trends, since the initial colonization by dispersing individuals precedes the establishment of a population with potential for further growth and expansion. Once colonization has succeeded, the spatial pattern of animal abundance is associated with intra- and interspecific interactions and environmental factors (e.g., habitat and food availability) and the population shows similar demographic features throughout the whole occupation area, which has been called a diffusive dispersal pattern. Here, we analyze the current status of colonization by a guanaco population of ranches surrounding a protected area in Chilean Patagonia with data gathered along three consecutive years. We thus compared animal abundance and social structure between the protected and unprotected areas and evaluated throughout the whole area the effect of environmental factors on guanaco abundance, proportion of family groups, and reproductive success. Guanaco abundance significantly declined with increasing distance from the center of the local distribution and marginally with predation risk. Moreover, social structure showed only minor differences between areas, pointing to a diffusive dispersal pattern. These results suggest that the population is already well established and has the potential to grow and continue its expansion. The case exemplifies a challenging outcome of successful animal conservation, and it presents a useful approach to evaluate the state of wild ungulate populations colonizing new areas.

Keywords Population density · Abundance · Population dynamics · Population structure · Mammal dispersal

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Introduction

Animal conservation programs are successful in reversing negative population trends once the pressures involved in the decline of animal populations are removed. In this scenario, protected areas play a vital role for the recovery of threatened species (Fall and Jackson 2002; Hansen and DeFries 2007). In the case of species with large home ranges like many ungulates, the movement of animals towards surrounding non-protected zones is the natural outcome when populations increase within protected areas (Simonetti 1995; Gurd et al. 2001; Kowalczyk et al. 2013). Once unprotected areas have been colonized, conflicts with human activities can arise and some form of management of these buffer areas may be needed.

The dispersal of individuals away from the occupation area of a population is not a random event, and it can determine the

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spatial and demographic features of recently settled populations. The dispersal of large territorial ungulates frequently shows an ideal-despotic distribution (Fretwell 1972) where agonistic behavior among conspecifics is more intense at high densities and in more favorable habitats (Coulson et al. 1997; Pettorelli et al. 2003; Kjellander et al. 2004; McLoughlin et al. 2006). As a result, dominant individuals occupy territories of high quality and force subordinates to disperse to unoccupied, usually less-favorable areas (Fretwell 1972). Under this process, in the early stages of dispersal, the areas of recent colonization show (i) a higher proportion of juveniles, as they comprise the first wave of dispersers (Greenwood 1980; Sarno et al. 2003; Gaillard et al. 2008); and (ii) a lower density of families than in the source areas, since these are the dominant groups in several ungulate species (Greenwood 1980; Dobson 1982; Clutton-Brock and Coulson 2002). In this case, neither spatial patterns of animal density nor population social structure are dependent on environmental factors, but they are shaped by haphazard processes affecting individual dispersal events. Later in the colonization process, when the population is getting settled, the spreading adopts a diffusive pattern (Darmon et al. 2007) in which (i) animals concentrate close to the source of dispersers and their density diminishes with distance to the source according to a normal distribution (Skellam 1951); and (ii) demographic structure and age ratio become similar throughout the whole occupation area. In this situation, extrinsic factors like local resource availability, interspecific competition, and predation, as well as intrinsic factors like intraspecific competition, shape the spatial and social structure of populations (Coulson et al. 1997; Clutton-Brock and Coulson 2002; Andersen et al. 2004; Darmon et al. 2007).

Therefore, in the case of wild ungulate populations expanding from a protected area, the social and demographic structures are expected to differ between the settled fraction of the population and that occupying the expansion area. Under an ideal-despotic scenario within the protected site, any increase in the population density can trigger the rate of agonistic interactions between territorial males and juveniles and force the dispersal of the latter to the expanding edge of the distribution range (Dobson 1982; Howard 1986; Clutton-Brock and Coulson 2002; Sarno et al. 2003). As a result, a higher proportion of juveniles, and a lower proportion of families should characterize the social structure in the expansion area. The production of yearlings should thus be proportionally lower in the dispersal area, and the reproductive rate can be even lower if the area is more stressful or less productive than the core of the distribution (Conradt et al. 1999). In addition to natural stressing factors, the settlement of a stable population is finally dependent on the species' ability to cope with human-derived effects, like competition with livestock or poaching. As a result of the dispersal and colonization process, human-wildlife conflicts can emerge in the expansion areas, especially with livestock farming, and they can trigger

negative pressures precluding wild population settlement (Simonetti 1995; Mishra et al. 2004; du Toit 2010).

The guanaco (*Lama guanicoe*) is the largest South American ungulate, a wild camelid with resource-defense polygyny and a flexible social structure (Franklin 1983; González et al. 2006). Juveniles are expulsed from natal groups at the age of 1 year, and following expulsion, female juveniles usually add to other family groups while males form new or join other male groups (Franklin 1983). Thus, male groups are good indicators of dispersal in the species. Guanacos suffered a steep population decline after the Spanish arrival to South America attributed to overhunting, competition with domestic species and habitat degradation (Puig 1995; Baldi et al. 2016). During the last decades, guanaco conservation and management programs sponsored by governments have contributed to the recovery of the global population (Baldi et al. 2016). Currently, the main populations are located within protected areas of Patagonia and Tierra del Fuego, both in Argentina and Chile. There, the increasing pressure from private landowners of rangelands may result in a threat to the remaining high-density guanaco populations if management is not properly planned and implemented (Baldi et al. 2016; Hernández et al. 2017; Lambertucci and Speziale 2011). Of particular interest with these regards is the guanaco population located in Torres del Paine National Park (TdPNP) (Magallanes Region, Chile). The species was near extinction in this region in the mid-1970s (Franklin 1982), but guanaco protection policies since then allowed a large population increase, from less than 100 individuals in 1975 (Franklin 1982) to around 4200 in 2010 (Fig. 1). It is currently the second most important guanaco population in Chile after that one in Tierra del Fuego. This within-TdPNP population growth has occurred while causing an expansion outside of the protected area, where the species was absent for many decades (Franklin 1982; Iranzo et al. 2013). TdPNP is considered the main source of guanacos in the area (Franklin 1982; local landowners pers. com.). The first record of this expansion was described in 1995 (Sarno and Franklin 1999).

In this context, TdPNP and its surroundings offer a particular situation to analyze the spatial patterns and factors affecting the dispersal and settlement of an ungulate species around a protected area. Specifically, we first evaluate if guanaco abundance, social structure, and reproductive success along the whole area are associated to either (i) the distance from the core of the animal distribution, (ii) resource availability (primary productivity, availability of the most suitable habitats), (iii) potential competition with livestock (sheep abundance), or (iv) predation risk (relative abundance of the main predator). As explained above, factors shaping the spatial patterns of populations change from the dominance of (i) during the earlier stages of colonization, to that of (ii, iii, and iv) at later stages of the process or when already settled. Additionally, we test if guanacos inhabiting ranches

Fig. 1 Guanaco population censused in Torres del Paine National Park (TdPNP) between 1996 and 2010 (annual growth rate $r = 0.052$)
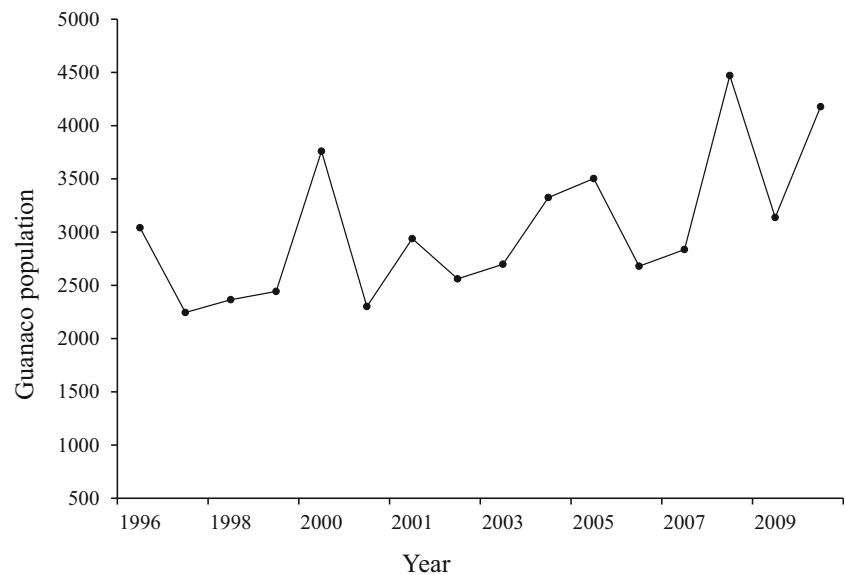
surrounding TdPNP show differences in their demographic characteristics in comparison with those within the protected area, paying special attention to male groups. In case animals are already firmly settled in the surroundings, no differences are expected throughout the occupation area in social and demographic structure indicators like the proportion of juveniles or that of family groups. Finally, to give the full picture of the guanaco population and its expansion process in the whole region, densities within and outside the protected area are compared and an updated estimation of population size is provided. This knowledge of the current status of the population (settled vs. in-expansion) and the ecological cues shaping guanaco distribution can provide useful tools for its management, and they exemplify the possible outcome of a wild ungulate population protected within a reserve that recovers from its initial low numbers.

Materials and methods

Study area

This study was conducted in Torres del Paine National Park and its surroundings, Southern Chile (51° 30′ S 72° 55′ W; Fig. 2). The study area covers approximately 1090 km² (284 km² within TdPNP and 806 km² belonging to neighboring ranches). Climate is temperate cool without a pronounced dry season. Annual rainfall varies between 300 and 1000 mm while mean temperature averages 2 °C in winter and 10.8 °C in summer (Vidal and Reif 2011). Vegetation in the study area is dominated by steppe-like grasslands and shrublands (Pisano 1974); a detailed description of vegetation communities can be found in Iranzo et al. (2013).

No livestock occurs within TdPNP. Oppositely, surrounding privately owned ranches are dedicated to extensive livestock farming, consisting mainly of sheep (see below). TdPNP is delimited by a 1.2-m-high wire fence which restricts livestock movements but acts only as a semipermeable barrier to wildlife movement (Rey et al. 2012).

Animal data collection

Two-person observer teams with binoculars conducted six seasonal field surveys to estimate abundance and social structure of guanacos within and outside TdPNP during the austral winter (July) and late spring-summer (December) of three consecutive years (2009–2011). Observer teams surveyed simultaneously in each occasion all roads, tracks and footpaths existing within ($N_{transect} = 15$; total transect length = 114.8 km; range, 3.1–26.2 km) and outside TdPNP ($N_{transect} = 17$; total transect length = 221.8 km; range, 0.7–17.3 km). Surveys took place during daylight hours avoiding periods of poor visibility at dawn and dusk. Surveys along roads were conducted by car driven at a nearly constant speed of 15 km/h, while tracks and paths (22.5 km only within TdPNP) were surveyed on foot. Both methods are comparable since they do not disturb animal behavior or habitat selection in the study area, where animals show short flight distances (Malo et al. 2009; see also Iranzo et al. 2013; Traba et al. 2017, for similar procedures). To avoid double counts in adjacent transects, only groups contained within a perpendicular boundary to the transect end were recorded (similar to a saw-tooth sampling design; Buckland et al. 2001). From a conservative perspective, assuming a 400-m band width with complete detection on either side of the road (Pedrana et al. 2009), the sampled area corresponds to 24.7% of the whole study area (Fig. 2).
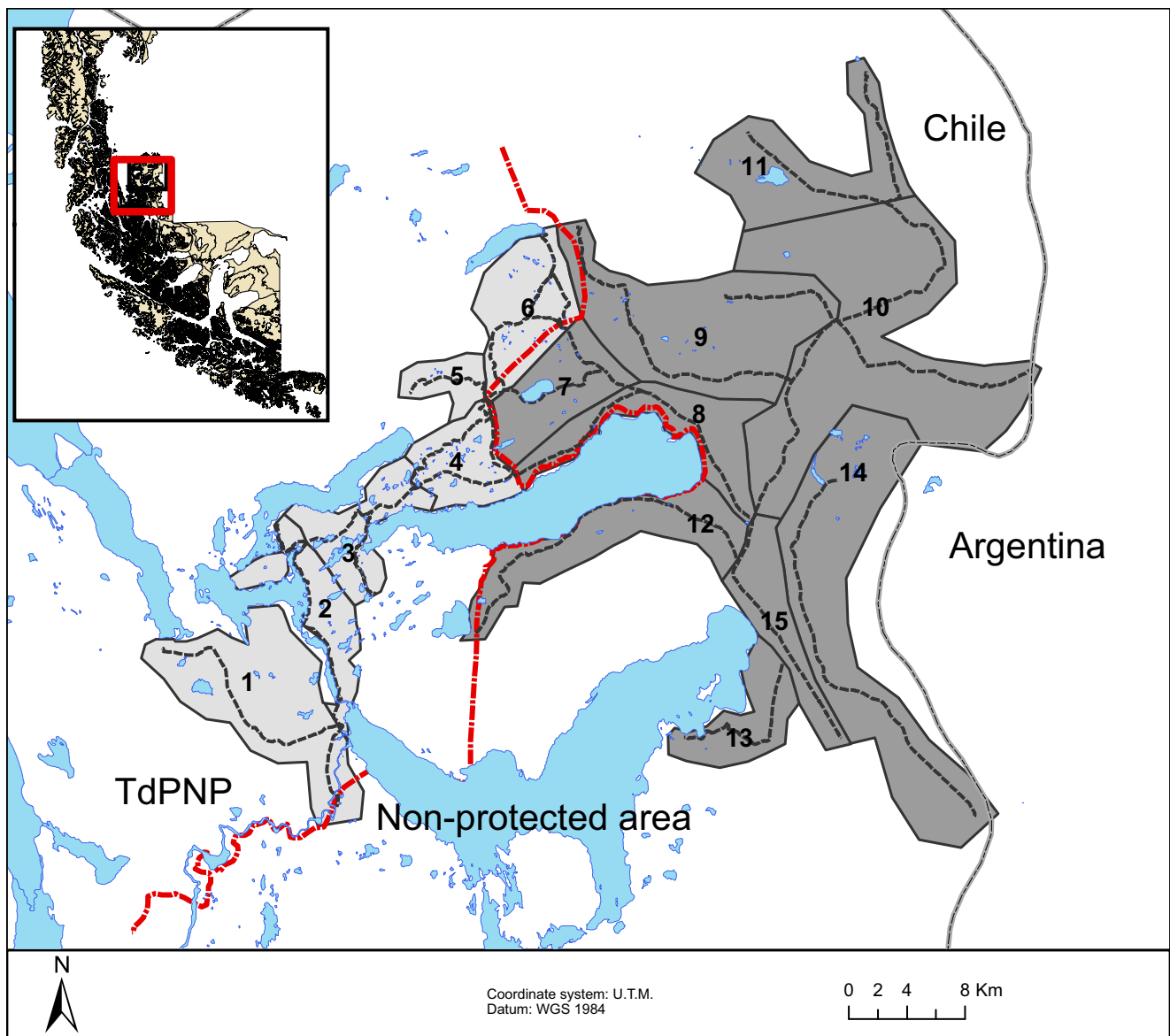
Fig. 2 Location of the study area in the Comuna Torres del Paine (Magallanes Region, Chile) and distribution of transects and sectors within the surveyed area

Following distance sampling protocols (Buckland et al. 2001), we recorded locations for every guanaco (solitary individuals and social groups) encountered using a GPS, measured the distance to the central point of groups using a laser rangefinder (Leica 1200RF), and determined the appropriate angle of our observations with a precision compass. In addition, we recorded group size, sex, and age class of all individuals. Individuals were classified into three age classes: adults (2 years and older), yearlings or juveniles (between 1 and 2 years) and chulengos (calves up to 1 year old) (Franklin 1983). According to Franklin (1982), we assigned observations of guanacos to one of the following social groups when all the individuals within a group were accurately identify (otherwise, they were assigned as undetermined groups): (i) family groups formed by a territorial male with females and

their offspring, (ii) solitary territorial males, (iii) groups of juveniles and mature non-territorial males. Some juvenile females may also join the so-called male groups (pers. obs.), though they are still mostly males, and (iv) female groups consisting of adult females with or without chulengos or yearling females without an adult male. Out of the breeding season, guanacos tend to form large mixed herds composed of adults of both sexes, yearlings, and chulengos (Franklin 1982; González et al. 2006), although all four social units mentioned above may still be encountered. In our study area we recorded solitary males, male groups, female groups, and mixed groups during winter.

The guanaco is a sexually monomorphic ungulate (Sarno and Franklin 1999) and sexual assignments are thus dependent on the corroboration of the presence of testicles and by

reproductive behavior, as tail rising (Franklin 1983; Ortega and Franklin 1995). Thus, despite guanaco groups can be seen and accurately located at long distance (more than 1200 m, own data), sexual (and age) correct assignments are subject to high uncertainty above 400 m (Pedrana et al. 2009). Consequently, all observations above this threshold were used for density estimations but removed for social structure analyses.

Environmental data

In order to estimate the effect of both density-related (intra- and interspecific competition), and environmental factors (resource availability, predation risk and distance to the core of the local distribution) on guanaco abundance, proportion of family groups and reproductive success (chulengo/adult ratio), we recorded data on (i) primary productivity, (ii) habitat suitability, (iii) puma (*Puma concolor*) relative abundance (predation pressure), and (iv) livestock abundance (proxy of anthropic perturbations and interspecific competition). Previously, we divided the study area into 15 different sectors, attending to topographic and physiognomic similarity. Each sector included 1 to 4 of the above-mentioned transects (see Fig. 2; Table S1). Each sector was large enough to harbor a good representation of the different habitats present in the study area and to have a large enough number of animals to adequately test the hypotheses (see Traba et al. 2017).

To account for the potential effect of primary productivity on guanaco abundance and distribution we used the Normalized Difference Vegetation Index (NDVI) value. NDVI values were obtained using MODIS-Terra images (MOD13Q1/Terra Vegetation Index 16Day L3 Global 250m SIN Grid V005) acquired during a 16-day period in December 2012 and July 2013 for summer and winter data, respectively. The persistent cloud cover prevented from using the same period as that for field sampling. However, it should have no effect on our results since the analysis is focused to inter-sector differences.

Grasslands (both natural and artificial) and *vegas* (meadows in the proximity of shallow wetlands) are considered the most suitable habitats for guanaco in the study area (Iranzo et al. 2013) due to their productivity and good visibility to detect predators (Bank et al. 2003). To estimate the cover of suitable habitat we located two control sampling points every 1000 m of each transect alternately right/left at 250 and 100 m distance from it ($N = 194$ sampling points in TdPNP, $N = 394$ sampling points in non-protected area in winter; $N = 222$ sampling points in TdPNP, and $N = 366$ points in non-protected area in summer). At each sampling point, we described the proportion (percentage of cover) of the above-mentioned suitable habitats in a plot of 50 m radius (see Iranzo et al. 2013 for further details).

Puma surveys were conducted using footprints on snow during the winters of 2011 and 2012 along the whole are covered with guanaco surveys. A 200 × 5-m line was walked every 5000 m of each of the above-mentioned guanaco surveys transects, and all marks of puma presence were recorded to build an index of kilometric abundance (KAI; Vincent et al. 1991) of puma per sector. Puma home ranges in the study area are small (19.0–84.5 km²) and tend to remain spatially constant throughout the year (Barrera et al. 2010), thus allowing the use of winter data as a proxy of puma relative abundance also in summer, when footprint surveys are unfeasible. In addition, roads are regularly used by pumas in this area (own unpublished data), and therefore useful as sampling method (Van Dyke et al. 1986; Van Sickle and Lindzey 1992).

Livestock abundance was recorded in parallel to guanaco surveys. Location and group size of livestock herds were used to calculate the KAI of livestock per transect, year and season. Similarly, we used guanaco sightings to calculate the KAI of guanaco per transect, year and season.

Statistical analyses

Factors influencing guanaco abundance, proportion of family groups and reproductive success.

Factors influencing guanaco abundance, proportion of family groups, and reproductive success among the 15 sectors were analyzed through General Linear Models (GLM) fitted for the following response variables: abundance of guanacos in each season and, only for summer data, proportion of family groups and chulengo/adult ratio of families (Table 1). Abundance of guanacos and sheep per sector were estimated by averaging transect and year KAIs to estimate mean KAI for each sector and season. In a similar way, the average percentage of family groups and chulengo/adult ratio of family groups were estimated for each sector only in summer. We also computed the average NDVI for each sector and season in a 400-m buffer around each transect. This was the same area used to estimate guanaco and sheep KAIs. A similar procedure was used to estimate intensity of use by puma, although in this case, we only have one estimate for both seasons. Habitat suitability was estimated as the mean proportion of grasslands and *vegas* per sector, averaging data from control points within each sector and season (Table 1).

In order to evaluate the effect of the distance of each observation to the core of animal distribution, we first estimated the geographical centroid of all animal observations weighted by group size for each season. We then calculated the distance from each observation to this seasonal centroid, using ArcGis 9.3 (ESRI 2007) for both calculations. Finally, to obtain a unique value per sector we averaged all the distances per sector and season (Table 1).

We obtained models for each response variable (guanaco abundance in summer and winter, and chulengo/adult ratio

Table 1 Raw values for the response and environmental explanatory variables per sector for the factors influencing guanaco abundance and reproductive success analyses

Sector	Zone	Length (km)	Family group	C/A ratio	NDVI winter	NDVI summer	Suitable habitat (%)	Dist centr. winter (km)	Dist centr. summer (km)	Guanaco winter	Guanaco summer	Sheep winter	Sheep summer	Puma
1	TdPNP	22.2	0	0	0.312	0.424	26.58	36.6	31.9	0	0	0	0	1.5
2	TdPNP	20.4	1.00	0.39	0.520	0.640	5.13	30.9	24.9	0.1	0.8	0	0	1.1
3	TdPNP	17.0	0.19	0.24	0.227	0.424	8.36	26.2	18.8	11.9	1.8	0	0	6.3
4	TdPNP	25.7	0.26	0.26	0.306	0.391	21.56	18.5	10.5	26.5	26.9	0	0	2.1
5	TdPNP	7.5	0	0	0.345	0.405	58.47	20.0	8.7	22.9	0.3	0	0	5.0
6	TdPNP	22.0	0.17	0.21	0.313	0.481	33.29	17.1	4.4	48.2	31.2	0	0	1.6
7	Outside	18.4	0.34	0.35	0.352	0.540	29.57	12.6	2.9	10.4	50.8	4.3	0	0.6
8	Outside	23.8	0.20	0.10	0.377	0.614	26.61	4.5	8.8	34.5	8.8	89.8	3.9	0.6
9	Outside	33.2	0.41	0.39	0.311	0.560	46.36	8.7	9.1	21.3	9.9	83.4	54.7	0
10	Outside	47.2	0	0	0.336	0.459	30.30	11.8	20.6	6.7	1.4	85.4	129.5	0
11	Outside	22.4	0.50	0.07	0.259	0.489	44.25	19.8	20.6	20.0	6.0	93.1	172.0	0
12	Outside	26.2	0.28	0.36	0.352	0.443	31.99	10.9	13.4	25.1	11.6	35.3	110.2	0
13	Outside	13.5	0.10	0.17	0.397	0.432	50.75	18.8	27.8	37.9	44.0	125.2	16.0	0
14	Outside	18.6	0	0	0.319	0.544	32.14	15.2	27.5	1.8	0.2	93.6	151.1	0
15	Outside	18.5	0.33	0.33	0.317	0.533	63.63	12.6	23.4	16.9	5.2	79.4	229.8	0.2

Length, total transect line surveyed per season (km); Family group, proportion of family groups in summer; C/A ratio, chulengo/adult ratio in summer; Suitable habitat, proportion of grasslands, and vegas; Dist centr winter, distance to the centroid of winter observations (km); Dist centr summer, distance to the centroid of summer observations (km); Guanaco winter, kilometric abundance index (KAI) of guanacos in winter (animal/km); Guanaco summer, KAI of guanacos in summer (animal/km); Sheep winter, KAI of livestock in winter (animal/km); Sheep summer, KAI of livestock in summer (animal/km); Puma, relative puma abundance (KAI; tracks/km)

and proportion of family groups only in summer) by performing GLM forward-backward stepwise regression on all the predictors that were included in each predictor-set model (Márquez et al. 2011). For each response variable, the full model included the distance to the centroid of animal distribution, NDVI, proportion of suitable habitats, abundance of livestock and intensity of use by puma. Proportion of suitable habitats showed significant Pearson correlation with several variables, so we decided to exclude it from the analyses. Inclusion of variables in the stepwise selection of predictor-set and combined models was based on significance testing. Additionally, the stepwise approach has recently been suggested as one of the best methods to describe species distributions based on different sets of predictors (Barnagaud et al. 2012). All variables were transformed to meet normality assumptions and standardized. Proportion variables were arc-sin transformed, count variables were square root transformed and continuous variables were log-transformed. We used the free software R version 3.2.1 (R Core Team 2014) and lme4 package (Bates et al. 2015) to conduct GLMs.

Social structure

Groups including individuals with unknown sex or age (undetermined groups, hereinafter) were excluded from the analyses; they accounted for 23% of the observed groups in winter (corresponding to 16% of all animals) and 11% in summer (12% of all animals). These proportions are similar to those provided by Pedrana et al. (2009) for large-scale road surveys.

We first describe typical group size since this metric complements mean group size and provides more information about grouping trends (White et al. 2012). Then, we tested for basic differences in social structure. We used factorial ANOVA and a posteriori Tukey test to evaluate differences in group size for each social group among years, seasons, and zones (within/outside TdPNP). In addition, we tested for differences in guanaco reproductive success (chulengo/adult ratio of family groups) among years and zones by factorial ANOVA and a posteriori Tukey test, only with summer data. All data were transformed to meet test assumptions, but untransformed data are shown in the text to facilitate interpretation.

We used GLM with a binomial distribution to test for differences in social structure (i.e., proportion of each type of social unit) among years, seasons and zones. We built four different response variables: (i) family groups vs. all other groups, (ii) solitary males vs. all other groups, (iii) male groups vs. all other groups, and (iv) female groups vs. all other groups. We included three different explanatory factors: year

(2009, 2010, 2011), season (winter, summer), and zone (within and outside TdPNP), and their biologically relevant interaction, season × zone, in the analyses. We confirmed that model assumptions were met and selected the best model for each response variable based on AIC (Akaike 1974). These statistical analyses were performed with INFOSTAT 2013 (Di Rienzo et al. 2011).

Population abundance and density

Finally, we used program DISTANCE (version 6.0; Thomas et al. 2010) to obtain updated estimates of population density (*D*) and abundance (*N*) of guanacos. We estimated population parameters separately for each year, season and zone (within and outside TdPNP). To avoid bias related to road sampling, we estimated guanaco abundance only for the whole study area. We further screened our data for additional possible bias in detection probabilities related to road survey or animal behavior following Thomas et al. (2010). All observations further than 1200 m (above the range of the rangefinder) were removed for DISTANCE analyses.

We analyzed distance data using conventional (CDS) and multiple covariate (MCDS) methods (Buckland et al. 2001) and considered three functions in density estimation: uniform, half-normal, and hazard-rate (Buckland et al. 2001). We used the cosine adjustment function for all analyses. We built models both using exact perpendicular distances, and by grouping perpendicular distances into intervals of 50 and 100 m in order to improve model fit. We included the number of individuals in each sighting as a covariate since detectability can vary depending on group size. Model selection was based on Akaike Information Criterion (AIC; Akaike 1974). Differences in abundance and density among years, seasons and zones (within and outside TdPNP) were analyzed via factorial ANOVA only for main effects using INFOSTAT 2013 (Di Rienzo et al. 2011).

Results

Factors influencing guanaco abundance, social structure, and reproductive success

Distance to guanaco centroid and puma intensity of use were included in the final model to explain guanaco abundance in summer (adjusted *R* squared = 0.404; $F_{2, 11}$ = 5.39; *p* = 0.023; Table 2). During summer, guanaco abundance was negatively related to the distance to the distribution centroid (Fig. 3a) and negatively related to intensity of use by puma, though at a statistical marginal level (Fig. 3b). No other factors affected guanaco abundance during this season.

Final model to explain guanaco abundance during winter included only one variable (distance to winter centroid), and was

Table 2 Final GLM forward-backward stepwise regression models for guanaco abundance during winter and summer within and outside Torres del Paine National Park (Chile)

Guanaco abundance	Estimate	Std. error	*t* value	*p* value
Summer				
Intercept	2.369	0.493	4.802	< 0.001
Distance to summer centroid	− 1.119	0.401	− 2.790	0.018
Puma	− 0.894	0.426	− 2.096	0.060
Winter				
Intercept	2.943	1.093	2.692	0.021
Distance to winter centroid	− 1.245	0.548	− 2.272	0.041

significant but less explanatory than summer model (adjusted *R* squared = 0.313; $F_{1, 13}$ = 3.13; *p* = 0.070; Table 2). During
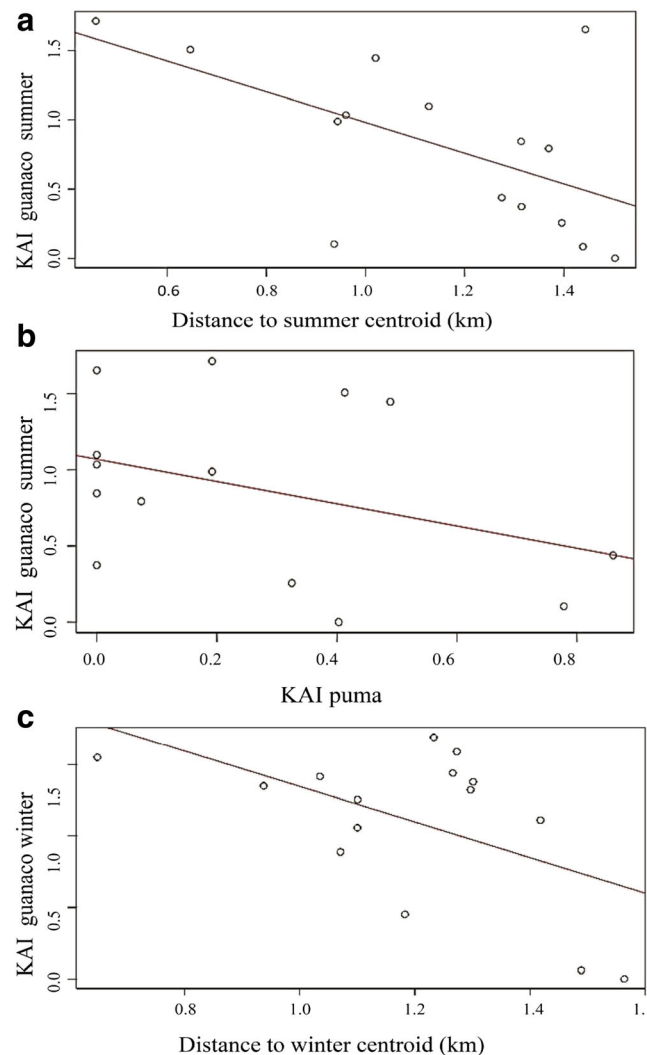

Fig. 3 Relationships of guanaco abundance with **a** distance to the centroid of summer distribution, **b** puma abundance, and **c** distance to the centroid of winter distribution. Fitted lines from linear regression are shown

winter, guanaco abundance was marginally and negatively related to the distance to the centroid of the distribution (Fig. 3c), and all other factors showed no relationship with guanaco abundance.

Both summer and winter centroids of observations were located outside the TdPNP, 3 km and 400 m away from the border, respectively. During summer, the proportion of family groups and the chulengo/adult ratio (averaging 0.22 at a global scale) showed no relationship with any of the considered factors.

Social structure

After excluding undetermined groups, solitary males were the most frequent social unit in summer (55%), followed by family groups (26%), male groups (17%), and female groups (2%). In winter, mixed groups were the most frequent social units (54%), followed by solitary males (25%), male groups (15%), and female groups (6%). Family groups gathered the highest proportion of animals in summer (64% of all animals), and mixed groups in winter (94% of all animals), followed by male groups (29 and 4% of all animals in summer and winter respectively). Solitary males represented 6% of all animals in summer and 1% in winter, while female groups were unfrequently observed.

Proportion of family groups varied between zones (Table 3), and it was higher outside (mean ± SE = 0.43 ± 0.03) than within TdPNP (0.36 ± 0.02). Proportion of male groups also differed between zones, and it was again higher outside (0.20 ± 0.02) than within TdPNP (0.13 ± 0.02; Table 3). On the contrary, the proportion of solitary males was higher within TdPNP (0.56 ± 0.03) than outside (0.32 ± 0.03), and it was higher in summer (0.54 ± 0.02) than in winter (0.25 ± 0.03; Table 3). Finally, proportion of female groups was higher in winter (0.06 ± 0.004) than in summer (0.01 ± 0.02; Table 3).

Regarding family groups in summer, mean group size ranged between 2 and 90 guanacos (mean ± SE = 16.6 ± 0.8; median = 11), and it did not vary between zones or years. In these groups, number of adults ranged between 2 and 66 adults (13.5 ± 0.9; median = 9); number of chulengos varied between 0 and 26 (3.5 ± 0.2; median = 2); and number of yearlings varied between 0 and 8 (0.6 ± 0.08; median = 0). Typical family group size was 38.6 animals, composed of 25.1 adults, 9.8 chulengos, and 3.7 yearlings. During this season, the chulengo/adult ratio showed differences among years (ANOVA: $F_{2, 201}$ = 8.39, $p < 0.001$) and marginal differences between zones (ANOVA: $F_{1, 201}$ = 3.79, $p = 0.053$). This ratio was larger in 2009 and 2010 (0.34 ± 0.03, and 0.32 ± 0.02, respectively) than in 2011 (0.20 ± 0.03), and slightly larger outside (0.32 ± 0.02) than within TdPNP (0.26 ± 0.02). Male group size, although highly variable (mean ± SE = 13.16 ± 2.4; median = 3; range 2–210 guanacos; typical size = 92.1) did not differ between zones, seasons, nor years ($p > 0.05$). Finally, female group size (mean ± SE = 5.1 ± 1; median = 3; range 2–25 guanacos) did not show differences between zones, seasons, nor years ($p > 0.05$).

Table 3 Factors affecting the proportion of each type of guanacos social unit within and outside Torres del Paine National Park (Chile) in winter and summer during 2009–2011

Model	χ^2	p value
Family group		
Intercept	0.07	
Year	2.54	0.240
Zone	8.31	0.004
Male group		
Intercept	1.77	
Year	4.77	0.090
Season	1.09	0.300
Zone	9.53	0.002
Season*zone	1.87	0.170
Solitary males		
Intercept	0.79	
Year	1.81	0.450
Season	65.34	< 0.001
Zone	26.41	< 0.001
Season*zone	0.04	0.850
Female group		
Intercept	2.70	
Year	3.28	0.190
Season	13.93	< 0.001
Zone	0.13	0.720
Season*zone	3.30	0.070

GLZ with binomial distribution were used

Population abundance and density

Over six seasons, 2121 groups of guanacos were sighted, with a total of 30,515 individuals counted. Total seasonal number of sighted animals varied from 3187 to 4561 individuals during summer (mean ± SE = 4038 ± 743) and 5570 to 6697 individuals during winter (6134 ± 564; Table 4). In every survey, more animals were recorded outside than within TdPNP. Regarding the number of sightings, more groups were consistently detected in summer than in winter (Table 4).

The estimated total abundance of guanaco ranged from 13,000 animals to 17,000 in summer and from more than 13,000 to almost 22,000 animals in winter (Table 5). Despite this variation, estimates of guanaco abundance showed no significant differences among years or seasons ($p > 0.05$).

Estimates of population density varied across years and seasons (range summer = 10.2–25.6 individuals/km^2; range winter = 8.3–36.6 individuals/km^2; Table 5), although no significant differences were found. Differences in guanaco density between within and outside TdPNP were significant, being larger within TdPNP than outside ($F_{1, 7}$ = 12.01; $p < 0.01$; range within = 16.3–36.6 individuals/km^2; range outside = 8.3–14.5 individuals/km^2; Table 5).

Table 4 Guanacos (and groups) recorded in each social unit sighted within and outside Torres del Paine National Park (TdPNP) in winter and summer during 2009–2011

Year	Season	Zone	Family group	Male group	Solitary males	Female group	Undetermined group	Total/zone	Total/season
2009	Winter	Within TdPNP	1534 (22)	41 (6)	16 (16)	16 (3)	480 (20)	2087 (67)	5570 (225)
		Outside TdPNP	1033 (41)	68 (7)	6 (6)	31 (5)	2345 (99)	3483 (158)	
	Summer	Within TdPNP	1202 (46)	395 (23)	126 (126)	5 (2)	30 (5)	1758 (202)	4365 (462)
		Outside TdPNP	1125 (81)	809 (44)	91 (91)	10 (4)	572 (40)	2607 (260)	
2010	Winter	Within TdPNP	2626 (41)	32 (8)	14 (14)	0 (0)	133 (11)	2805 (74)	6697 (262)
		Outside TdPNP	2056 (71)	70 (7)	28 (28)	8 (3)	1730 (79)	3892 (188)	
	Summer	Within TdPNP	888 (42)	272 (17)	122 (122)	14 (5)	174 (21)	1470 (207)	4561 (503)
		Outside TdPNP	1364 (81)	244 (26)	79 (79)	2 (1)	1402 (109)	3091 (296)	
2011	Winter	Within TdPNP	1292 (24)	13 (5)	16 (16)	13 (2)	259 (20)	1593 (67)	6135 (223)
		Outside TdPNP	1752 (41)	129 (11)	17 (17)	29 (3)	2615 (84)	4542 (156)	
	Summer	Within TdPNP	667 (38)	311 (25)	97 (97)	6 (4)	54 (18)	1135 (182)	3187 (446)
		Outside TdPNP	804 (48)	249 (26)	56 (56)	0 (0)	943 (134)	2052 (264)	

Discussion

Our results support the existence of a large guanaco population in the area that shows a diffusive dispersal pattern embracing the Torres del Paine National Park and its surroundings. Overall, guanaco abundance declined with increasing distance to the geographic centroid of the distribution, both in summer and winter, and showed some association with environmental variables as expected under a late phase of the dispersal process (Skellam 1951; Darmon et al. 2007). Analysis of social structure also reinforces this result, as the differences in the proportion of male groups between the source and the colonization area are still present, but other demographical indicators like the proportion and size of family groups, or the chulengo/adult ratio point to the presence of a firmly established population outside the protected area.

We detected some marginal association between the spatial patterns of guanaco abundance and puma use during summer, which point to a population in a late-phase of dispersal. Under this phase of dispersal, we expected a significant relationship between guanaco abundance, proportion of families or reproductive success, and environmental factors as they are traditionally considered crucial factors explaining ungulate abundance (Andersen et al. 2004). However, no one of the environmental variables different than the distance to the core of the distribution was included neither in the winter nor the summer models, excepting the puma relative abundance during summer. This could be explained by an early-phase of dispersal, when animal spatial pattern and density are not environmentally restricted, but randomly shaped (Greenwood 1980; Dobson 1982; Clutton-Brock and Coulson 2002; Gaillard et al. 2008). However, the negative relationship of guanaco abundance with puma relative

Table 5 Density (animals/km²) estimated of guanaco within and outside Torres del Paine National Park (Chile), and abundance of guanacos for the whole study area (within TdPNP + outside TdPNP) in winter and summer during 2009–2011

Year	Season	Zone	Selected model	n	D	N total	CV
2009	Winter	Within TdPNP	Hazard-rate intervals 100 m	65	17.6	13,381	29
		Outside TdPNP	Hazard-rate	113	10.4		
	Summer	Within TdPNP	Hazard-rate intervals 100 m	200	25.0	17,034	27
		Outside TdPNP	Hazard-rate intervals 100 m	191	12.3		
2010	Winter	Within TdPNP	Hazard-rate intervals 100 m cluster size as covariable[a]	73	36.6	17,051	–
		Outside TdPNP	Hazard-rate intervals 100 m cluster size as covariable[a]	155	8.3		
	Summer	Within TdPNP	Hazard-rate intervals 100 m	206	25.6	15,931	27
		Outside TdPNP	Hazard-rate intervals 100 m	243	10.8		
2011	Winter	Within TdPNP	Hazard-rate cluster size as covariable[a]	66	36.3	21,966	–
		Outside TdPNP	Hazard-rate cluster size as covariable[a]	143	14.5		
	Summer	Within TdPNP	Hazard-rate intervals 100 m	183	16.3	13,009	28
		Outside TdPNP	Hazard-rate intervals 100 m	219	10.2		

Final distance model selected

n, number of detections; D, guanaco density (guanaco/km²); N, abundance estimated; CV, percent coefficient of variation of abundance estimated for each year, season, and zone

[a] Models with cluster size as covariate do not provide CI (95%)

abundance during summer points to a primary factor driving animal distribution, that is the avoidance of higher predation risk areas (Acebes et al. 2013). Summer is the birth season, when predation on chulengos is higher and guanaco try to reduce predation risk (Acebes et al. 2013). Besides, guanaco is a generalist herbivore that can occupy habitats poor in resources and withstand harsh environmental conditions (González et al. 2006; Puig et al. 2008; Acebes et al. 2013), which could have masked other purely environmental associations. Further analyses should help to identify other important environmental variables involved in guanaco abundance and reproductive success (Hopcraft et al. 2010; McLoughlin et al. 2006).

Analyses of social structure offer contradictory results. On the one hand, the reported mean and typical family group size in summer are among the largest ever described for the species (Puig and Videla 2007; Rey et al. 2009; Taraborelli et al. 2012). This, together with the high animal density found within the protected area, point to a crowding effect potentially occurring in the TdPNP (Sutherland and Norris 2002; Marino et al. 2016). Tight aggregation of animals is expected to increase agonistic interactions among them, forcing juveniles and subordinates to disperse (Greenwood 1980; Lawson Handley and Perrin 2007). Accordingly, the proportion of male groups was higher outside TdPNP than inside, as expected for an early-phase dispersal population under an ideal-despotic scenario (Fretwell 1972). Male group size was similar between zones and comparable with those previously observed in Torres del Paine (Ortega and Franklin 1995).

On the other hand, the proportion of family groups was higher outside TdPNP than within it, which suggests a later stage of the dispersal process with reproductive units already settled in the expansion area. In fact, the chulengo/adult ratio during summer, although relatively low compared with other populations (see e.g. Acebes et al. 2013), was slightly larger outside TdPNP, pointing again to a well-established population there. Therefore, the population growth can be expected to continue and this expectation is in accordance with (i) the increase in the population reported within TdPNP with respect to that described in previous years by CONAF (Fig. 1), and (ii) the fact that densities estimated within TdPNP (16.3–36.6 guanacos/km^2) are among the highest ever reported for the species (Sarno and Franklin 1999; Burgi et al. 2012).

The aggregated spatial distribution of animals can address large uncertainty in DISTANCE software outcomes (Thomas et al. 2010; Hema et al. 2017), reflected in wide coefficient of variation for abundance estimations. Despite this, distance sampling method is recommended against total counts or fixed-width strip transect methods that tend to underestimate population numbers (Buckland et al. 1993). Still being cautions due to road sampling and the coefficient of variation for abundance estimations, our results help illustrate the successful re-colonization of an species whose occurrence was anecdotic 40 years ago and is currently abundant (see also Olson et al. 2005; Durant et al. 2011;

Gallardo et al. 2010; Travaini et al. 2015; Hema et al. 2017). In fact, our features point to more than a 100-fold increase in abundance in this period (Franklin 1982; Sarno and Franklin 1999).

Moreover, more than half of the guanaco population inhabits the neighboring ranches of TdPNP, though at a lower density there than within the protected area. Even so, density reported outside TdPNP (8.3–14.5 guanacos/km^2) is also among the highest described for guanaco populations outside protected areas (Burgi et al. 2012; Schroeder et al. 2014). Although no definitive conclusion about the actual origin of the living-outside animals can be argued from our results, movements from protected areas towards surrounding ranches after a population growth have already been reported in other wild ungulate species (Madhusudan 2004; Plumb et al. 2009; Kowalczyk et al. 2013; Jung 2017), suggesting a similar phenomenon in this case, as reported by Sarno and Franklin (1999).

From an applied perspective, the analysis of the demographic parameters and the distribution of animals around the centroid shown here can be useful to evaluate the state of wild ungulate populations whose protection within protected areas has been effective and led to populations colonizing the surrounding areas. With this set of parameters and the reported results, it is possible to conclude with some certainty that the guanacos outside the protected area are already established (large numbers, large proportion of family groups), and the population has the potential to grow and continue its expansion (similar reproductive success outside than within TdPNP). All together, they put forward the heated situation in which landowners of surrounding private lands will feel the guanaco as a competing species that should be controlled. Indeed, a management program to control the population of guanacos has recently started in the surroundings of the National Park in order to address these complaints and reduce the conflict with livestock farming, the most widespread socio-economic activity in the area.

References

Acebes P, Malo JE, Traba J (2013) Trade-offs between food availability and predation risk in desert environments: the case of polygynous monomorphic guanaco (Lama guanicoe). J Arid Environ 97:136–142

Akaike H (1974) A new look at the statistical model identification Automatic Control. IEEE Trans 19:716–723. https://doi.org/10.1109/tac.1974.1100705

Andersen R, Herfindel I, Sæther BE, Linnell JD, Oddén J, Liberg O (2004) When range expansion rate is faster in marginal habitats. Oikos 107:210–214

Baldi R, Acebes P, Cuéllar E, Funes M, Hoces D, Puig S, Franklin WL (2016) Lama guanicoe. The IUCN Red List of Threatened Species 2016 doi:https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T11186A18540211.en. Accessed 19 Aug 2016

Bank MS, Sarno RJ, Franklin WL (2003) Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biol Conserv 112:427–434

Barnagaud J-Y, Devictor V, Jiguet F, Barbet-Massin M, Le Viol I, Archaux F (2012) Relating habitat and climatic niches in birds. PLoS One 7:e32819

Barrera K, Soto N, Cabello J, Antúnez D (2010) El puma. Antecedentes para su conservación y manejo en Magallanes. Servicio Agrícola y Ganadero, Punta Arenas

Bates D, Maechler M, Bolker M, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman & Hall, London

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling. Oxford University Press, London

Burgi MV, Marino A, Rodriguez MV, Pazos G, Baldi R (2012) Response of guanacos Lama Guanicoe to changes in land management in Peninsula Valdes, Argentine Patagonia: conservation implications. Oryx 46:99–105. https://doi.org/10.1017/s0030605311000214

Clutton-Brock T, Coulson T (2002) Comparative ungulate dynamics: the devil is in the detail. Philos Trans R Soc B: Biol Sci 357:1285–1298

Conradt L, Clutton-Brock TH, Guinness FE (1999) The relationship between habitat choice and lifetime reproductive success in female red deer. Oecologia 120:218–224

Coulson T, Albon S, Guinness F, Pemberton J, Clutton-Brock T (1997) Population substructure, local density, and calf winter survival in red deer (Cervus elaphus). Ecology 78:852–863

Darmon G, Calenge C, Loison A, Maillard D, Jullien J-M (2007) Social and spatial patterns determine the population structure and colonization processes in mouflon. Can J Zool 85:634–643

Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M, Robledo CW (2011) InfoStat

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

du Toit JT (2010) Addressing the mismatches between livestock production and wildlife conservation across spatio-temporal scales and institutional levels. In: Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems. p. 30

Durant SM, Craft ME, Hilborn R, Bashir S, Hando J, Thomas L (2011) Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. J Appl Ecol 48:1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

ESRI (2007) GIS and mapping software. http://www.esri.com/

Fall MW, Jackson WB (2002) The tools and techniques of wildlife damage management—changing needs: an introduction. Int Biodeterior Biodegrad 49:87–91

Franklin WL (1982) Biology, ecology, and relationship to man of the South American camelids. In: Mammalian biology in South America. 6:457–489

Franklin WL (1983) Contrasting socioecologies of South America's wild camelids: the vicuña and guanaco. In: JFK E, Kleiman DG (eds) Advances in the study of mammalian behavior. The American Society of Mammalogists, USA, pp 573–629

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton

Gaillard JM, Hewison AJ, Kjellander P, Pettorelli N, Bonenfant C, Van Moorter B, Liberg O, Andren H, Van Laere G, Klein F, Angibault JM (2008) Population density and sex do not influence fine-scale natal dispersal in roe deer. Proc R Soc Lond B Biol Sci 275:2025–2030

Gallardo G, Nuñez A, Pacheco LF (2010) Line transects as an alternative to estimate vicuna (Vicugna vicugna) abundance: case study at the Sajama National Park, Ecol Bolivia-Rev 45(1):64–72

González BA, Palma RE, Zapata B, Marín JC (2006) Taxonomic and biogeographical status of guanaco Lama guanicoe (Artiodactyla, Camelidae). Mammal Rev 36:157–178. https://doi.org/10.1111/j.1365-2907.2006.00084.x

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Gurd DB, Nudds TD, Rivard DH (2001) Conservation of mammals in eastern North American wildlife reserves: how small is too small? Conserv Biol 15:1355–1363

Hansen AJ, DeFries R (2007) Ecological mechanisms linking protected areas to surrounding lands. Ecol Appl 17:974–988. https://doi.org/10.1890/05-1098

Hema EM, Di Vittorio M, Barnes RFW, Guenda W, Luiselli L (2017) Detection of interannual population trends in seven herbivores from a west African savannah: a comparison between dung counts and direct counts of individuals. Afr J Ecol. https://doi.org/10.1111/aje.12397

Hernández F, Corcoran D, Graells G, RÕos C, Downey MC (2017) Rancher perspectives of a livestock-wildlife conflict in Southern Chile. Rangelands 39:56–63

Hopcraft JGC, Olff H, Sinclair ARE (2010) Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends Ecol Evol 25:119–128

Howard PC (1986) Spatial organization of common reedbuck with special reference to the role of juvenile dispersal in population regulation. Afr J Ecol 24:155–171. https://doi.org/10.1111/j.1365-2028.1986.tb00357.x

Iranzo EC, Traba J, Acebes P, González BA, Mata C, Estades CF, Malo JE (2013) Niche segregation between wild and domestic herbivores in Chilean Patagonia. PLoS One 8:e59326. https://doi.org/10.1371/journal.pone.0059326

Jung TS (2017) Extralimital movements of reintroduced bison (Bison bison): implications for potential range expansion and human-wildlife conflict. Eur J Wildl Res 63:35. https://doi.org/10.1007/s10344-017-1094-5

Kjellander P, Hewison AJM, Liberg O, Angibault JM, Bideau E, Cargnelutti B (2004) Experimental evidence for density-dependence of home-range size in roe deer (Capreolus capreolus L.): a comparison of two long-term studies. Oecologia 139:478–485

Kowalczyk R, Krasińska M, Kamiński T, Górny M, Struś P, Hofman-Kamińska E, Krasiński ZA (2013) Movements of European bison (Bison bonasus) beyond the Białowieża Forest (NE Poland): range expansion or partial migrations? Acta Theriol 58:391–401

Lambertucci SA, Speziale KL (2011) Protecting invaders for profit. Science 332:35–35

Lawson Handley L, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. Mol Ecol 16:1559–1578

Madhusudan M (2004) Recovery of wild large herbivores following live-stock decline in a tropical Indian wildlife reserve. J Appl Ecol 41:858–869

Malo J, González B, Traba J, Estades C, Acebes P, Galaz J, Zapata B (2009) Modulation of guanaco (Lama guanicoe) flight behaviour by tourist use in Torres del Paine region. In: 10th international mammalogical congress, Mendoza, Argentina. pp 134–135

Marino A, Rodríguez V, Pazos G (2016) Resource-defense polygyny and self-limitation of population density in free-ranging guanacos. Behav Ecol 27:757–765

Márquez AL, Real R, Olivero J, Estrada A (2011) Combining climate with other influential factors for modelling the impact of climate change on species distribution. Clim Chang 108:135–157

McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. Proc R Soc Lond B Biol Sci 273:1449–1454

Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA, Prins HHT (2004) Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. J Appl Ecol 41:344–354. https://doi.org/10.1111/j.0021-8901.2004.00885.x

Olson KA, Fuller TK, Schaller GB, Odonkhuu D, Murray MG (2005) Estimating the population density of Mongolian gazelles Procapra gutturosa by driving long-distance transects. Oryx 39:164–169. https://doi.org/10.1017/S0030605305000402

Ortega IM, Franklin WL (1995) Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Rev Chil Hist Nat 68:489–500

Pedrana J, Rodríguez A, Bustamante J, Travaini A, Zanón Martínez JI (2009) Failure to estimate reliable sex ratios of guanaco from road-survey data. Can J Zool 87:886–894

Pettorelli N, Gaillard JM, Duncan P, Maillard D, Van Laere G, Delorme D (2003) Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology 84:3307–3316

Pisano E (1974) Estudio ecológico de la región continental sur del área andino patagónica. II Contribución a la fitogeografía de la zona del Parque Nacional Torres del Paine. vol 5

Plumb GE, White PJ, Coughenour MB, Wallen RL (2009) Carrying capacity, migration, and dispersal in Yellowstone bison. Biol Conserv 142:2377–2387. https://doi.org/10.1016/j.biocon.2009.05.019

Puig S (1995) Técnicas para el manejo del guanaco. IUCN, Buenos Aires

Puig S, Videla F (2007) Distribución, densidades y estado de conservación de los camélidos. In: Martinez Carretero E (ed) Diversidad biológica y cultural de los altos Andes Centrales de Argentina. Editorial Fundación Universidad Nacional de San Juan, Argentina, p 198

Puig S, Videla F, Cona MI, Roig VG (2008) Habitat use-by guanacos (Lama guanicoe, Camelidae) in northern Patagonia (Mendoza, Argentina). Stud Neotropical Fauna Environ 43:1–9. https://doi.org/10.1080/01650520701461319

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rey A, Carmanchahi PD, Puig S, Guichón ML (2009) Densidad, estructura social, actividad y manejo de guanacos silvestres (Lama guanicoe) en el sur del Neuquén, Argentina. Mastozool Neotropical 16:389–401

Rey A, Novaro AJ, Guichón ML (2012) Guanaco (Lama guanicoe) mortality by entanglement in wire fences. J Nat Conserv 20:280–283

Sarno RJ, Franklin WL (1999) Population density and annual variation in birth mass of guanacos in southern Chile. J Mammal 80:1158–1162

Sarno RJ, Bank MS, Stern HS, Franklin WL (2003) Forced dispersal of juvenile guanacos (Lama guanicoe): causes, variation, and fates of individuals dispersing at different times. Behav Ecol Sociobiol 54:22–29

Schroeder NM, Matteucci SD, Moreno PG, Gregorio P, Ovejero R, Taraborelli P, Carmanchahi PD (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

Simonetti JA (1995) Wildlife conservation outside parks is a disease-mediated task. Conserv Biol 9:454–456. https://doi.org/10.1046/j.1523-1739.1995.9020454.x

Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 38:196–218

Sutherland WJ, Norris K (2002) Behavioural models of population growth rates: implications for conservation and prediction. Philos Trans R Soc Lond Ser B Biol Sci 357:1273–1284

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

Thomas L et al (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14. https://doi.org/10.1111/j.1365-2664.2009.01737.x

Traba J, Iranzo EC, Carmona CP, Malo JE (2017) Realised niche changes in a native herbivore assemblage associated with the presence of livestock. Oikos 126:1400–1409. https://doi.org/10.1111/oik.04066

Travaini A, Zapata SC, Bustamante J, Pedrana J, Zanón JI, Rodríguez A (2015) Guanaco abundance and monitoring in Southern Patagonia: distance sampling reveals substantially greater numbers than previously reported. Zool Stud 54:23

Van Dyke FG, Brocke RH, Shaw HG (1986) Use of road track counts as indices of mountain lion presence. J Wildl Manag 1:102–109

Van Sickle WD, Lindzey FG (1992) Evaluation of road track surveys for cougars (Felis concolor). Great Basin Nat 1:232–236

Vidal OJ, Reif A (2011) Effect of a tourist-ignited wildfire on Nothofagus pumilio forests at Torres del Paine biosphere reserve, Chile (Southern Patagonia). Bosque 32:64–76

Vincent JP, Gaillard JM, Bideau E (1991) Kilometric index as biological indicator for monitoring forest roe deer populations. Acta Theriol 36:315–328

White P, Gower CN, Davis TL, Sheldon JW, White JR (2012) Group dynamics of Yellowstone pronghorn. J Mammal 93:1129–1138