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How density-dependence and climate affect guanaco population dynamics

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ABSTRACT

The guanaco (*Lama guanicoe*) is one of the two South American native wild camelid species, and despite its important ecological role and economic value conservationists are in a permanent conflict with sheep ranchers. Currently, management programs are being developed in Argentina and Chile to guarantee guanaco and grassland conservation. We developed a non-linear simulation, three stages-structured matrix model of guanaco population dynamics, with climatic and density-dependence effects, that can be used as a tool to devise optimal management interventions. We estimated population parameters using a 41-year time-series data from a guanaco population in Tierra del Fuego (Chile). We conducted a multivariate multiple regression analysis between matrix demographic parameters (survival at each stage and fertility) as dependent variables, and climatic variables and population density as independent variables.

Guanaco density was significantly correlated with female newborn and adult annual survival while annual precipitation correlated significantly with the fertility (females born per female per year), in contrast to population regulation mechanisms commonly seen in other ungulate species. This guanaco model allows the evaluation of the effects of different events (e.g. offtake, particular dry or wet years, poaching) on specific sexes and life stages which is the field information commonly available.

1. Introduction

The guanaco (*Lama guanicoe*), one of the two wild camelid species of South America, is a seasonal breeder with a resource defence polygyny mating system (Franklin, 1983, 1982). It has an average gestation period of 11.5 months, gives birth to only one offspring per female per season, and breeds in summer within a couple of weeks following parturition, from December to mid-February (Franklin, 1982). In the wild, females breed for the first time at 2+ years of age (Raedeke, 1979). Currently the guanaco occupies only 26% of its original range (Baldi et al., 2016), and its range distribution has been reduced by 60% in Argentina, 75% in Chile (Franklin et al., 1997), and over 90% in Perú, Bolivia, and Paraguay (Cunazza et al., 1995); additionally its distribution has become fragmented having small, relatively isolated populations (Baldi et al., 2016). However, this species was not considered as a threatened species but was assigned a Least Concern status in the IUCN Red List of Threatened Species (Baldi et al., 2016) based upon its wide continental distribution (around one million km^2), its presumed total population size (around one million adults), and the presence of numerous protected areas across its range of distribution. For the same reasons, the guanaco has been included in Appendix II of CITES (CITES, 2015), which implies the regulation of international commerce of meat and fine-fiber products to insure that such trade does not threaten the guanaco's survival by requiring that management plans have been put in place. This species has high conservation interest and economic value, and it is embedded in socioeconomic and political conflicts between conservation groups and sheep ranchers (Baldi et al., 2016). This conflict results from an apparent guanaco-sheep competition for food and water resources (Baldi et al., 2001, 2004). Currently, different management programs are being developed in Argentina and Chile in an attempt to resolve this unsettled situation and guarantee both guanaco and grassland conservation. Nonetheless, those management programs do not evaluate possible effects of potential management actions and environmental influences on the population dynamics of guanacos because, although there are some works which considered age-structured models for this species in the Chilean island of Tierra del Fuego (Franklin and Fritz, 1991), and elsewhere (Rabinovich, 1995), there are no studies showing how density dependent processes and

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climatic factors may differentially affect guanaco age or stage classes.

Density-dependence has been incorporated in population models since the conception of the logistic model of population growth. Dennis and Taper (1994) proposed a discrete, density-dependent, stochastic, logistic model to test the existence of density-dependence processes. This model and others derived from it are still frequently used for demographic studies as well as for wildlife management (Keyser et al., 2006; Hostetler et al., 2013). However, models that differentiate individuals by sex, age or stage can be more useful when comparing different management strategies; as expressed by Gordon et al. (2004): "the long-term population dynamics research has revealed fundamental differences in how sex/age classes are affected by changes in density and weather. Consequently, management must be tailored to the age and sex structure of the population, rather than to simple population counts".

Structured demographic models are useful because they provide explanations of population dynamics in terms of the fates of individuals in each class. Mentis (1977) objected to the use of non-structured logistic-type population models to estimate the maximum harvestable yield because "the harvesting is likely to alter the age distribution and therefore r", and Caswell and Fujiwara (2004) consider that in age- or stage-structured models, modelling relationships between a species' life cycle and its population dynamics is richer and more realistic. In the logistic population model the optimal per capita harvest rate to achieve maximum sustained yield is $h = r/2$ (r being the intrinsic rate of population increase) while in a stage-structured model it is $h = r/\lambda$ (λ being the finite rate of population growth) (Williams et al., 2002).

Many years have passed since structured models began to be used to describe population dynamics; Leslie (1959) proposed the first stage-structured model with a linear restriction on survival from one age to the next as a function of the population size. Jensen (1995) developed a variation of the matrix model of Liu and Cohen (1987), based on a discrete time form of the logistic equation, that was successfully applied to a grey wolf population in a limited environment (Miller et al., 2002).These structured models have also become usual tools in conservation biology and wildlife management; e.g., Jensen (1996) developed a harvest model for white-tailed deer (*Odocoileus virginianus borealis*) based on a density-dependent matrix model to determine the maximum sustainable yield, evaluate the effect of harvest on fecundity and survival of each age group, and to estimate the age structure of the optimum yield. In the case of South American camelids there only a few non-age-structured models (Rabinovich, 1985; Shaw et al., 2012; Zubillaga et al., 2014; Marino et al., 2014), and only two age-structured population matrix models that have been developed for guanacos (Franklin and Fritz, 1991; Rabinovich, 1995); however, none of them included density-dependent and climate components. These two components are very important in ungulate dynamics, particularly for species that show relatively low fecundity and long longevity, as is the case of guanacos; it was found that in this kind of species usually a depression of both fecundity and survival results with increases in population density, particularly in winter time (Clutton-Brock et al., 1997), determining their particular dynamic population pattern.

We used a stage-structured model to test the hypothesis that both density-dependence and climatic processes regulate and/or limit guanaco populations. We also used this model to determine which guanaco stage class is more sensitive to density-dependent or climatic factors, and set the grounds for its future use as model to inform management decisions.

2. Materials and methods

2.1. Study area

We used a 41 year-long time series (1977–2017) of data from a wild guanaco population sampled in the 2000 km^2 Cameron ranch (53.9 °S, 69.3 °W), located in the central-northern part of the Island of Tierra del Fuego, Chile, at an altitude of 0–300 m. The area has a mean annual precipitation of 370.6 mm (SD = 51.8) and a mean annual temperature of 6.55 °C (SD = 0.35). It is characterized by undulating terrain, with abundant streams and valleys and presence of peat bogs in the lower elevations. A single major river (the Río Grande) runs through the area. The region is a mosaic of steppe ("pampa") and forest biomes; the latter is composed by deciduous forests dominated by "lenga" (*Nothofagus pumilio*) and "ñire" (*N. antartica*). The steppe is composed of species of *Stipa, Festuca, Berberis*, *Baccharis*, *Empetrum, Azorella, Trifolium*, *Agrostis, Poa*, *Hordeum* grasses, as well as species of Juncacea and Cyperacea, and of the genera *Carex* and *Sphagnum* (peat bogs). On Tierra del Fuego island, guanacos are not preyed upon by pumas (*Puma concolor*) as they are in continental populations (Soto, 2010). See Zubillaga et al. (2014) for more detailed information on the study site.

2.2. Field sampling

Counts of visible guanacos took place during the post-reproductive period (February–April) and lasted approximately 7 days. Counts occurred daily between 10:30 and 19:00 h, with two observers in each of two 4 × 4 vehicles driving the main, secondary and local roads at a maximum speed of 40 km/h. Each road was covered only once and particular care was taken to avoid duplication of counts at road intersections. Guanacos were counted for 41 consecutive years between 1977 and 2017, with the exception of years 1986 and 1996; for those two years, we linearly interpolated the population count using counts from the adjacent years. From 1977 to 2000 a transect with a variable width was used to spot guanacos, and from 2001 to 2017 a transect with a fixed width band of 500 m to each side of the transect was used (Tellería, 1986; Davis and Winstead, 1987; Caughley, 1980; Buckland et al., 1993). In addition to individual guanaco counts, the following were recorded for each observation: weather conditions, time, distance (km) from the starting point, coordinates, observation distance from the transect (m), and an estimate of the angle to the animals' locations; when the animals were observed in groups the number of individuals, and the social type of the group (family groups constituted by an territorial male, several females and their offspring; bachelor groups, constituted principally by non-reproductive juvenile and adult males; and solitary males, Franklin, 1982, 1983), were also recorded, as well as its age-class structure (newborns, juveniles, and adults). There are other minor variations on this classification in social units of Patagonian guanacos, like mixed groups, and female groups (Ortega and Franklin, 1995; Iranzo et al., 2018), but the one we used covers the dominant social units, and the easiest to recognize in the field. The road network and all geo-referenced observations were processed with the ArcView 9.3 Geographical Information System (GIS), and transferred to a spreadsheet using program Map Source. Cartography was kindly provided by the Agriculture and Livestock Service from Chile. Despite randomly selected transects are recommended (Eberhardt, 1978), pre-existing roads were used because according to Soto (2010) the existing system of roads cover an adequate sample of the whole area. The area effectively surveyed in each sampling period was around 420 km^2, which represents about 20% of the study area.

Existing roads may not comply with the requirement of random transects to survey wildlife populations; however, in the case of the area occupied by the guanacos in Tierra del Fuego (Chile) two field surveys were made comparing guanaco counts using existing roads with guanaco aerial surveys based on systematic transects. One such comparison was made in the area of the Río Cóndor Forest Project (Forestal Savia Ltda., 2002), and the second in San Gregorio Commune, Province of Magallanes (Corcoran and Graells, 2015; SAG, 2015). The results of the former field comparison showed that the aerial survey estimated 11% less guanacos than the road survey, but no detailed information to estimate a statistical significance of this difference was provided. The latter resulted in aerial population estimate of 63,540 guanacos, while the road survey resulted in a population estimate of 62,692 guanacos

(range 59,058–66,327); the road count range includes the population estimated with the aerial survey, providing the necessary assurance that the guanaco road count can be considered acceptable. On the other hand, neither the road counts nor the aerial surveys estimate guanaco numbers in the forested areas, because of the low visibility there, but at the time when the annual surveys are carried out, most of the guanaco population is found in the grasslands. Additionally, as the regulations in Chile prohibit hunting along roads, the annual variations in hunting pressure should not affect guanaco counts that are made along existing roads.

The population size was estimated as given in Soto (2010) which was based on the King method modified by Leopold (1933) and described by Raedeke (1979); the population estimate (N) is given by:

$$N = \frac{A * n}{2 * y * x}$$

where A is the total study area, n is the total number of animals counted, x is the total transect distance covered rounded to one meter, and y is the average of the perpendicular distance from the transect to the animals counted (the factor of 2 is included to consider that there is one band to each side of the transect). The variance (S^2) of the population estimate is given by:

$$S^2 = \frac{n}{p^2} * \frac{1-p+n}{n+2}$$

with p = n/N; this variance was used to estimate the 95% upper and lower confidence intervals.

Soto (2010) compared population estimates by the Leopold and Distance methods, and found that the value of the means estimated by the Leopold method fall within the confidence intervals estimated by the Distance method; all sampling periods used the same field methodology.

In the case of "undetermined" animals or social units in the survey, we distributed them into each of the three social units (family groups, bachelor groups, and solitary males) using the 41-years average proportion of each of these social units.

2.3. Data analysis

2.3.1. Outlier analysis

Time series outliers may have important impacts on population model predictions (Trívez, 1994); we searched for possible outliers using the "*tsoutliers*" package in R (Lopez de Lacalle, 2014; R Version 3.2.1, www.r-project.org) for non-linear time series (Chen and Liu, 1993). This package can be applied to seasonal and non-seasonal autoregressive-moving average (ARMA) processes, detecting types and effects of outliers, and their location. Outliers can be classified in four types according to their effect on the series. Given the dynamic process of the guanaco the outliers the use of "additive outliers" (AO) of the "*tsoutliers*" package was justified: events (an external effect) affect a time series in a single instant of time and causes an immediate and one-shot effect on the observed series (Trívez, 1994; Chen and Liu, 1993). Once an AO was detected we "corrected" it by averaging the population estimates from the previous and following years.

2.4. Population matrix model

We used a female-only, stage-structured matrix population model (Lefkovitch, 1965). According to their size and behaviour female guanacos were differentiated in three classes: newborns (individuals aged 0–1 years), juveniles (individuals aged 1–2 years, not sexually mature), and adults (individuals > 2 years-old, sexually mature). Although guanaco males may reach sexual maturity at over 3 years old when testes are functional, and some females (> 2 yrs old) may become mature if they are over 80% of their adult body weight, the former cannot be represented in a female-only model, and the latter represents only a small fraction of the female juvenile population.

The projection matrix ($\boldsymbol{A}$) has the fertility in the first row and last column (indicating that only adults reproduce), the annual survival of individuals of each stage in the diagonal, and the annual transition probabilities between stages in the sub-diagonal (Caswell, 2001). The projection matrix we used is given by:

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & f \\ S_N & 0 & 0 \\ 0 & S_J & S_A \end{bmatrix}$$

where f is fertility (female newborns per adult female per year) and S_A represents female adult annual survival. As the newborn and juvenile stages last 1 year, their transition probabilities are the survival from one year to the next, represented by S_N and S_J, respectively.

The projection operation can be written as:

$$\boldsymbol{n}_{(t+1)} = \boldsymbol{A} * \boldsymbol{n}_{(t)} \quad (1)$$

where $\boldsymbol{n}_{(t)}$ is a vector with the number of female individuals in each age class, at time t. We used a model step time (projection interval), t, of 1 year. For each simulation period we sum each stage of the female population vector ($\boldsymbol{n}$) to obtain the total female population. We estimated the total population (female and male) multiplying the female model predictions by 2, because the newborn sex-ratio is 1:1 (Franklin and Johnson, 1994), and we found no reliable information suggesting differential survival between male and female individuals (Sarno et al., 1999; Sarno and Franklin, 1999).

2.4.1. Parameter estimation

We implemented the population matrix model in an Excel® spreadsheet, with one population matrix for every year of data, and parameterized the four matrix coefficients for each year of data. To estimate the annual matrix coefficients, we used the Solver tool in Excel® spreadsheet (version 2010) minimizing separately the sum of the square error (SSE) between field counts and model predictions of newborns on one hand, and of pooled juvenile and adult classes on the other hand; the latter procedure was used because the field identification between juveniles and adults wasn't as reliable as that of the newborns. The pool of the juvenile and adult classes was made exclusively for the purpose of having a more consistent goodness of fit measure, and does preclude the use of a three-stage projection matrix model, and because it results in a more accurate fecundity estimation: a pool of juvenile and adult females in one stage class (leading to a 2 × 2 stage matrix population model) would under-estimate the fecundity because juveniles are a non-reproductive class. Since from a time series of t years only t-1 transition matrices are possible, from our 41 years-long time series, we obtained 40 projection matrices. The four matrix parameters of the 40 matrices were estimated simultaneously by the Solver tool (i.e., the 160 parameters were simultaneously modified in each iteration). We used the Generalized Reduced Gradient (GRG) non-linear option of Solver, which usually converged to a minimum SSE in between one to five minutes of computing time. We constrained the possible annual survival coefficient estimates to be ≤ 0.99 and the adult female fertility estimates to be ≤ 0.5, because they are the biological maxima for these parameters.

During the time period of the field guanaco population data series there were 13 seven events of adult guanaco harvests (years 1980, 1982, 1999, 2003, 2005, 2006, 2010–2015 and 2017, with harvests of 100, 100, 69, 1700, 2000, 2000, 1500, 1461, 2176, 2220, 1804, 401 and 988 individuals, respectively). To include the harvest events in our model we subtracted the number of field harvested adult individuals from the modelled adult population at simulated time ($t + 1$), because in the field the population is sampled before it is harvested, so that the effects of the harvest become manifest in the population when sampled at the following year.

2.4.2. Sensitivity and elasticity analysis

We carried out a sensitivity analysis to evaluate the influence of the each of the four matrix model parameters on the finite population growth rate (λ). Because transition probabilities and fertility are measured on different scales, we also conducted an elasticity analysis to measure proportional sensitivity (Caswell, 2001). The elasticity analysis was carried out for each annual projection matrix to evaluate possible elasticity changes among years, using the *PopTools* application for Excel® (version 2010).

2.5. Density-dependent and climatic factors

To test our hypothesis that density-dependent processes and climatic factors regulate and limit guanaco population size, respectively, we used the point estimates of the annual projection matrix coefficients, and tested statistically their possible relationship with total annual guanaco density estimates, the sheep presence and climatic factors.

The projection matrix coefficients cannot follow a normal distribution because they are asymmetric and also truncated on both tails. We therefore checked the underlying statistical distribution of all four matrix coefficients. We fitted the 40 years of the projection matrix coefficient estimates to four statistical distributions: the normal distribution and three non-symmetric distributions: Weibull, Gamma, and lognormal using the *fitdistrplus* package in R (Delignette-muller and Dutang, 2015), with a special modification to account for the particular case of truncated data (C. Dutang, personal communication) using the "*truncdits*" package in R (Novomestky et al., 2016). When more than one statistical model resulted in a statistically significant fit, we selected the "best" one based on the Akaike Information Criterion (AIC).

We evaluated the possible effect of density and/or climate on the projection matrix coefficients by a multiple multivariate regression analysis (MMRA) and a multivariate analysis of variance (MANOVA), to account for correlations among responses (Friendly, 2007). MMRA fixes experiment-wide error rates, and the significance level, α, is adjusted to account for simultaneous testing of many variables to maintain the overall α at the level set by the researcher (Rencher, 2002).

To determine if the inter-annual variation of the matrix coefficients was related to density and/or climate variables, we used the stage-specific matrix coefficients as dependent variables; and as independent variables we selected the following: total guanaco population size, sheep abundance, annual precipitation, annual and winter temperature, annual precipitation with a lag of 1 year, annual and winter temperature with a lag of 1 year, 2-yr average annual precipitation, 3-yr average annual precipitation and total guanaco population size with a lag of 1 year. The winter period was from June to August. Because the population data come from a post-breeding survey (February–April) and annual climatic data were taken from January to December, we considered the lags in climatic effects as affecting the population counts in the following year.

Sheep abundance data were based on the time series shown in Zubillaga et al. (2014) and the series was extended until 2016 using information provided by the Agriculture and Livestock Service of Chile. Fifteen years of data were available (1980, 1985, 1990, 1995, 2000, 2005, 2006, 2008–2016), with sheep abundances of 45,000, 43,000, 41,000, 26,000, 35,000, 37,000, 37,227, 25,789, 45,370, 45,360, 19,900, 24,215, 26,075, 33,100, 30,025, and 27,271 animals, respectively. In 1995 an extremely harsh winter resulted in the death of 15,000 sheep in addition to the standing sheep count for 1995, so we corrected the 1995 sheep count to 41,000 sheep (26,000 sheep in 1995 plus 15,000 winter-killed sheep). Additionally sheep numbers changed smoothly between years (personal information by Mr. Dalmiro Guineo, 2011 administrator of Cameron ranch; Kevin Mac Lean, 2009 administrator of Cameron ranch, and Chilean Statistics of Agriculture and Livestock Service, 2006). We used the "*BaBooN*" package in R (Meinfelder et al., 2015), to conduct a Bayesian bootstrap predictive mean matching – multiple and single imputation algorithm, a procedure considered to be more efficient than parametric methods for discrete data when missing data are very abundant; we imputed the missing data between years with "*BaBooN*" package sheep estimates.

We used 29 years of climactic data (1974–2002) for the Cameron ranch from the Climatic Research Unit (CRU) TS 2.1 database, compiled by the Tyndall Centre, CRU, School of Environmental Sciences of the University of East Anglia, United Kingdom (http://www.cru.uea.ac.uk/cru/data/hrg.htm). Because the CRU data ended in 2002, we completed that time series from 2003 to 2017 with data from Punta Arenas (Chile), the closest meteorological station to Cameron ranch (≈340 km away). These data were downloaded from the Meteorological Service of Chile (http://www.meteochile.gob.cl/).

The MMRA method assumes no collinearity among the independent variables (Friendly, 2007). We checked for collinearity among the independent variables using the software STATISTICA (StatSoft, Inc. 2009, version 9.0. www.statsoft.com). We implemented the MMRA modelling using the package *candisc* (Friendly, 2007) in R, and used the statistically significant relationships obtained with the MMRA to select the independent variables correlated with the projection's matrix coefficients as multiplicative factors. Given that since 2010 the harvest was an annual (except for 2016) and with increased offtakes; we decided to carry out the analysis by time segments, in order to avoid the offtake masking the possible effect of density-dependence or of climate. A first segment was 34 year-long (1977–2010) and a second segment included the last 15 years. As the response variables do not have normal distribution, a log-odds transformation was applied to the matrix coefficients (fertility and survival of newborns, juveniles, and adults).

Anticipating that the guanaco population could be regulated by the total guanaco population size, we considered the effect of density-dependence using seven different candidate functions (Bellows, 1981), and found that the Ullyett function (Ullyett, 1950) provided the most flexible sigmoid form of density-dependence. This function was implemented replacing N_t (population size) by the variable *DPK* (Eq. (2)).

$$DDf = \frac{1}{[1 + e^{(DPK-a)\times b)}]} \tag{2}$$

where *DDf* is the density dependent factor ($0 < DDf \leq 1$), *DPK* is the density of the guanaco population expressed as a proportion of its carrying capacity (*K*), and *a* and *b* are parameters to be estimated. As an estimate of *K* we used the result obtained by Zubillaga et al. (2014) for the guanaco population of Cameron ranch ($K = 46{,}563$ guanacos), which represents the average carrying capacity around which the population size fluctuates.

To incorporate the effects of climatic factors (*Clf*) in the simulation model we used a linear regression through the origin (Eq. (3)).

$$Clf = c * Cvar \tag{3}$$

where *c* is a parameter to be estimated, and *Cvar* are the climatic variables (precipitation or temperature). We expressed *Cvar* as a relative proportion, calculated as *Cvar* = 1+ ((annual value of the climatic variable – long term average of the annual climatic variable)/long term average of the annual climatic variable). Our definition of *Cvar* sums a value of "1" to the relative proportion to avoid negative numbers and allows it to be used as a multiplicative factor; this format also provides more generalizability to the climatic effects (i.e., it can be applied to a new location).

We estimated the *a, b* and *c* parameters of the density-dependent and climatic factor equations, using the Solver utility of Excel, applied to the average of the 40 values of the estimated matrix coefficients, in order to obtain a single set of values of the parameters *a*, *b* and *c*, which in the simulations is annually affected by the inter-annual variation of the model's covariates (total population density and precipitation or temperature). We calculated confidence intervals for these estimated parameters using a Monte Carlo simulation method, as proposed by Lambert et al. (2012).

Table 1
Mean, standard deviation (SD), lower and upper 95% confidence interval endpoints, coefficient of variation (CV) and the statistic distribution type (St. dist) of the four population matrix parameters used in the guanaco model: annual survival of newborns (S_N), juveniles (S_J) and adults (S_A), and the adult female fertility (f, as ♀ newborns/♀/year).

	Mean	SD	Lower CI	Upper CI	CV (%)	St. dist
f	0.24	0.08	0.11	0.42	33.5	gamma
S_N	0.73	0.13	0.48	0.97	17.9	lognormal
S_J	0.86	0.07	0.71	0.99	8.7	lognormal
S_A	0.92	0.06	0.76	0.99	6.8	weibull

3. Results

3.1. Data analysis

3.1.1. Outlier analysis

We found two outliers in the population time series: total population sizes of 33,125 guanacos for year 2007 and 56,973 guanacos for 2011 and we replaced them by the new values 56,895 and 45,073 guanacos, respectively (Table S1 in Supporting information).

3.2. Population matrix model

3.2.1. Population matrix parameter estimation

The estimated values of the 160 matrix coefficients (four coefficients for each of the 40 matrices) are given in Table S1 in the Supporting information. Table 1 shows the average and coefficient of variation of fertility and annual survival of newborns, juveniles, and adults, resulting in an intrinsic rate of natural increase of $r = 0.051$, and the population finite rate of growth was $\lambda = 1.052$ for this guanaco population.

3.2.2. Sensitivity and elasticity analysis

Using the average value of the matrix coefficients, the one with the highest impact on λ was adult survival (0.69), while juvenile survival, newborn survival, and fertility had the same, much lower impact (0.10). When using each of the 40 estimated annual transition matrices adult survival also had the strongest effect on λ (Table S2 in Supporting information).

3.3. Density-dependent and climatic factors

3.3.1. Collinearity analysis

Winter temperature (with and without lags) and precipitation (with and without lags), and total guanaco population size were not collinear, and were kept in the MMR analysis (Table S3 in Supporting information).

Sheep abundance was significantly and negatively correlated with guanaco abundance ($r^2 = -0.5$, $P < 0.0001$). We decided to keep the guanaco density as the independent variable for the MMRA because: 1) we wanted to evaluate the effect of the guanaco density on demographic parameters, 2) we didn't find any literature supporting the idea that sheep abundance causes a change in guanaco survival or fertility, and 3) the negative correlation between guanaco and sheep is likely to be related to guanaco avoidance of sheep and human activity rather than to a change in guanaco survival or fertility (Marino et al., 2016).

3.3.2. Multiple multivariate regression analysis

The MANOVA Pillai test statistic indicated for the first segment of the time series (1977–2010) that guanaco population size (N) was significantly ($P = 0.044$, test statistic = 0.314, approx. $F = 2.86$) correlated to S_N ($P = 0.035$) and S_A ($P = 0.016$), annual precipitation ($A.Pp$) was significantly correlated to f ($P = 0.026$); effect of population size on juvenile survival (S_J, $P = 0.90$) was considered too weak and was not included. For the final segment of the time series (2011–2017) no statistically significant effect of any independent variable was obtained.

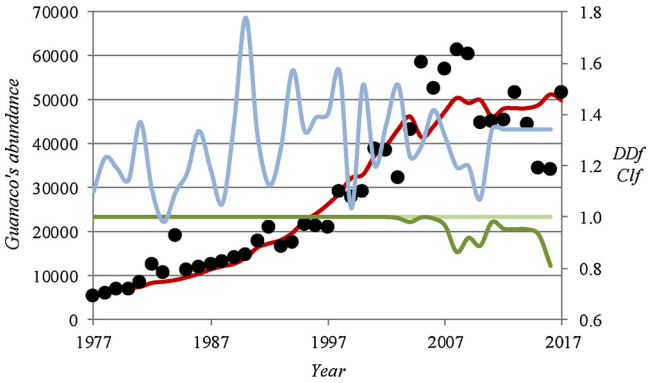

Fig. 1. Time series of the total guanaco population size (1977–2017), with field values (black dots) and simulated values based on the guanaco three-stage matrix population model (red line); climatic (*Clf*) (blue line) and density-dependent (*DDf*) (green line) factors were added to reflect the density-dependent population regulation and the climatic modulation effects, respectively (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

DDf was incorporated as affecting newborn and adult survivals and *Clf* affecting the fertility; so we fitted five parameters, two for each *DDf* and one for *Clf*. The Monte Carlo estimates of the parameters *DDf* function were: *a1* (median) = 1.79 (lower CI = 1.47, upper CI = 2.03) and *b1* (median) = 14.34 (lower CI = 12.09, upper CI = 16.08), *a2* (median) = 1.16 (lower CI = 1.09, upper CI = 1.35) and *b2* (median) = 22.51 (lower CI = 13.49, upper CI = 50.99), and the precipitation effect in the *Clf* function was *c* (median) = 1.27 (lower CI = 1.18, upper CI = 1.36).

The final non-linear, stage-specific population projection matrix with density-dependence and climate effects was:

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & 0.24 * Clf \\ 0.73 * DDf1 & 0 & 0 \\ 0 & 0.86 & 0.91 * DDf2 \end{bmatrix}$$

Predictions from this population model conformed well to the observed guanaco population, with population size fluctuating around the average carrying capacity (Fig. 1).

The range of *Clf* was 0.98 and 1.78 between all years resulting in an increase in fertility by up to 78% (highest precipitation values) and a decrease by down to 2% (lowest precipitation values). The "effective fertility" (i.e., average fertility*Clf) oscillated between 0.24 and 0.43 due to the effect of precipitation. The estimated *DDf* ranged between 0.81 and 1, leading to an adult survival decrease of 19% at high population densities.

4. Discussion

Analyses of vital rates and factors that affect them are often made by univariate methods, even if more than one dependent variable is evaluated. Univariate and multivariate analyses may give different results and lead to different conclusions (Friendly, 2007). MMRA is more appropriate than univariate multiple regression analysis for assessing potential relationships among several dependent and several independent variables and determining which of the independent variables should be incorporated in the final model. This is the first application of MMRA to a mammal population regulation analysis. We recommend this type of analysis to be applied to other mammalian populations analysis whenever several population parameters and various extrinsic conditions are available as time-series data for the same period.

There is a body of theory showing that the relationship between the guanaco counts and the matrix coefficients reflects a genuine relationship (Doak et al., 2005; Wisdom et al., 2000). Modelling the coefficients with part of the series and using the other part for validation purposes was initially considered, but two factors persuaded us against it: (a) the time series for parameter estimation and prediction verification would become too short, and (b) during those 40 years of data there is a marked trend from a very small initial population to a fairly large population oscillating around its carrying capacity; by splitting this time series in two parts would make impossible carried out the coefficients validation and would make impossible the detection of the observed trend from a small population, with an almost exponential population growth rate, to a high density population oscillating near its carrying capacity.

The demographic parameters estimated in our study seem to conform well to values available in the literature: in a guanaco study carried out in the San Pablo de Valdés Reserve (Chubut Province, Argentina) adult survival was 0.97, around 0.86–0.87 for newborns, and the average recruitment was 0.26 (0.18 and 0.32) (Marino et al., 2016). Likewise, Franklin and Fritz (1991) found that in Torres del Paine National Park, southern Chile, the annual survival of newborns, juveniles and adults was 0.74, 0.86 and 0.91, respectively, almost identical to the results of our matrix coefficient estimates for the Cameron ranch (0.73, 0.86 and 0.91, respectively). However, their estimate of the fecundity (female newborns per female) was higher (0.34) than the fecundity estimated at the Cameron ranch (0.24). Between 1991 and 1992 Gustafson et al. (1998) found that, also in Torres del Paine National Park, within the first 10 days of life the average survival of guanaco newborns was 0.85, which is a plausible value before reaching a lower survival of 0.74 after one year of life as newborns; however, we should remark that the main cause of mortality found by Gustafson et al. (1998) was the puma, which is not present in the Cameron ranch. Our results also conform well with the generalization that environmental variation and density dependence co-occur and have similar effects on various fitness components for large herbivore populations (Galliard et al., 2000). Interestingly this pattern is independent of body mass, taxonomic group, and ecological conditions. Our results also conform well with the general conclusions of Galliard et al. (2000), that adult female survival should show little year-to-year variation with CV < 10%, yearling survival should show moderate year-to-year variation with CV < 20%, and fertility should show strong variation with CV > 30%. However, our CV estimated for juvenile survival was 8.7%, while Galliard et al. (2000) indicated the CV for juvenile survival is often > 30%.This difference indicates a that survival of guanaco newborns seems more stable than in other ungulates; maybe as a result of the lack of important predators (the puma is absent in the Cameron ranch, and the human offtake is regulated to a relatively low level). More field studies, particularly with marked individuals, are necessary to evaluate the effect of these events on the guanaco population and elucidate this departure from theoretical expected results.

Some of the differences between our results and those found in some of the ungulate literature possibly reflect the difficulty in isolating climatic factors from density dependent effects, a serious problem encountered by Weladji et al. (2002) in the analysis of *Rangifer tarandus* and other ungulates. We believe that the relation between precipitation and guanaco fertility is well founded, since precipitation affects directly primary productivity and therefore on the availability of foraging resources and the nutritional state (condition) of females (Raedeke, 1979; Franklin, 1982). Additionally, Marino et al. (2016) suggest that there is no density-dependence on fertility.

The effect of density on adult survival has also been recorded in other large mammalian herbivore populations: in three African ungulates the effect of density on adult survival was evident above some threshold density (Owen-Smith, 2006). In our study density-dependence was detected only at high densities, roughly above 14 guanaco/km^2, because the *DDf* factor only differed from "1" when the population abundance was near its carrying capacity, as observed in other species such as the black rhino (Cromsigt et al., 2002). Moreover, our result that density-dependence affected mainly the female adult survival, conforms well with another of our results: that the guanaco population rate of growth is by far most sensitive to the guanaco female adult survival. From a biological and ecological standpoint this seems reasonable because adults are a class involving individuals up to 15–20 years of age, while the newborn and juvenile stages are composed of a one-year age class each. The function we used to represent the density-dependence process conforms well with non-linear density-dependent functions in population matrix models, such as the inverted logistic for survival (Pennycuick et al., 1968; Beddington, 1974); also flexible functions of this type have been widely used to describe the effect of density on different features of the life history (Watt, 1960).

The average carrying capacity of the guanaco population of the Cameron ranch based upon the last 17 years (when the population seemed to stabilize) was 46,694 guanacos (± 9384 std. dev.) which is quite similar to the 46,563 guanacos estimated in Zubillaga et al. (2014) using a non-structured mathematical model. The estimation of this parameter is of importance, for it is part of the density-dependent equation (see Eq. (2)). It should be noted that this estimation of carrying capacity is a BCC (Biological Carrying Capacity) and not a CCC (Cultural Carrying Capacity) *sensu* Minnis and Peyton (1995), which was applied to the guanaco-sheep conflict by Hernández et al. (2017).

Our exclusion of sheep abundance from the MMRA analysis doesn't mean that sheep management is not important for guanaco conservation. Guanaco abundance is likely to have a stronger effect than sheep abundance on guanaco demographic parameters, because there is a spatial segregation between guanacos and domestic herbivores (Schroeder et al., 2013; Hernández et al., 2017). We believe that the negative correlation between sheep and guanaco may reflect avoidance by guanacos of sites used by sheep rather than a possible effect of sheep on guanaco demographic parameters. This assumption is in accordance with the findings of Pedrana et al. (2010) who, using Species Distribution Modelling methods, found that the probability of guanaco occurrence decreased in places with moderate to high values of sheep abundance. Additionally, Messier (1994) showed that in the North American moose (*Alces alces*) there is a complex combined effect between density-dependent food competition and predation by wolves resulting in two density equilibrium conditions. The absence on the Cameron ranch of the puma, the main guanaco predator, simplified our analysis because we would not expect multiple equilibra.

Guanacos are known to behave both as sedentary animals as well as dispersing ones. For example, Iranzo et al. (2018) found that, in Torres del Paine National Park and its surroundings, in Southern Chile, guanaco abundance significantly declined with increasing distance from the center of the local distribution and marginally with predation risk, and that social structures showed only minor differences between areas, pointing to a diffusive dispersal pattern. These results suggest that the population in Torres del Paine National Park is already well established, and we believe that the Cameron ranch is in a similar condition. On the other hand, there are also seasonal movements: Novaro et al. (2009) estimated the seasonal abundance of guanacos and livestock using transect counts during 2005–2009 in the 450,000 ha Payunia reserve of Mendoza, Argentina, and observed that 63% (out of 17 individuals) of radio-collared guanacos migrated seasonally between summer and winter ranges. Neither of these two conditions would affect the population matrix model here used because the population estimates were made in the same month every year, and any potential individuals "lost" by dispersal would be compensated by potential individuals "added" also by dispersal.

We didn't take into account senescence (a decline of survival with increasing age). Bleu et al. (2015) found in two chamois populations that senescence responded differently to environmental variation in different age classes, suggesting that senescence patterns are not fixed

within a species. This process was also found in wild boar (*Sus scrofa*) females (Gamelon et al., 2014). These authors concluded that, in evolutionary terms, in ungulates the timing of senescence, not its rate, is associated with the magnitude of fertility. This is probably the situation for guanacos, with females showing a delayed onset of senescence and relatively low fertility. Although possibly data to test this process directly at our study site might exist because of the annually harvested animals, that data was not available to us, but we would expect the same pattern in guanacos, because guanaco individuals can obtain only a limited amount of energy, and thus cannot maximize both reproductive output and survival (Law, 1979), and as guanacos are considered reproductive throughout all their life (Raedeke, 1979) they may not have a reproductive senescent period.

The are several advantages of our stage-structured matrix model if it were applied to guanaco population management: the identification of age-groups makes the model more amenable to include other factors such as predation by puma and foxes that attack more frequently the newborns, a selective offtake (e.g., harvesting only adults, or only adults and juveniles), and poaching that usually go after adults (the largest individuals) for their weight in meat. Additionally, for the same reasons of being age-group specific, our model is also more amenable to an adaptive management framework, because testing, refining, and eventually improving the model's performance is facilitated by the age-group structure of the model because those age-groups are easily identifiable in the field.

In summary, we were able to disentangle the role of weather and density- dependence in the population regulation of guanacos on the Cameron ranch, Chile. Our results add a new example of the various ways in which ungulate species have responded to selection to their environment and evolved to maximize their fitness under climate uncertainty.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.07.010.

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