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RESEARCH ARTICLE

Density but not climate affects the population growth rate of guanacos (*Lama guanicoe*) (Artiodactyla, Camelidae) [version 1; peer review: 2 approved with reservations]

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Abstract

We analyzed the effects of population density and climatic variables on the rate of population growth in the guanaco (*Lama guanicoe*), a wild camelid species in South America. We used a time series of 36 years (1977-2012) of population sampling in Tierra del Fuego, Chile. Individuals were grouped in three age-classes: newborns, juveniles, and adults; for each year a population transition matrix was constructed, and the population growth rate (λ) was estimated for each year as the matrix highest positive eigenvalue. We applied a stepwise regression analysis with population growth rate (λ) as dependent variable, and total guanaco population (in natural logs), annual mean precipitation, and winter mean temperature as independent variables, with and without time lags. The effect of population size was statistically significant, but the effect of the climatic variables on guanaco population growth rate was not significant.

Keywords

Camelidae, climatic variables, density effects, guanaco, population regulation, population growth rate

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Any reports and responses or comments on the article can be found at the end of the article.

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Introduction

In order to understand population dynamics and optimize the management of wildlife populations it is important to identify how groups are affected by environmental factors and their own density, particularly in species living in extreme environments. Mechanisms that regulate populations of the guanacos (*Lama guanicoe*) are poorly known; this species is heavily exploited in the Patagonian steppe, and its numbers and distribution have diminished significantly during the last century because of grazing conflicts with a sheep-based society, and overhunting (the guanaco's historical distribution has been reduced by 75% in Chile and Peru, and by 60% in Argentina)¹. The guanaco is in the Least Concern IUCN Red List category (<http://www.iucnredlist.org/>, downloaded on 11 September 2013) but it has been included in Appendix II of CITES 2013 (<http://www.cites.org/eng/app/2013/E-Appendices-2013-06-12.pdf>).

No population of any species can grow indefinitely, and population checks based upon different processes restrict population size and/or geographic distribution; these processes are either density-stabilizing or density-limiting², the latter being independent of population size. Stabilization results from density-dependence, with a regulatory effect that varies in intensity with the size or density of the population itself. However, density-dependent processes are also affected by environmental conditions, and many wildlife population dynamic and management models include the effects of climatic covariates (e.g., Dennis & Otten, 2000; Colchero *et al.*, 2009)^{3,4}. In the case of the Ricker model (one of the most simple and most used population models), Corani and Gatto (2007)⁵ proposed an original way of incorporating climatic covariates: they were included as affecting the population growth rate.

The guanaco is one of the two extant wild South American camelids, and ranges from Northern Peru through Chile, and across Patagonia to southern Argentina and Chile, reaching Tierra del Fuego. It is found from sea level to nearly 4500 m on the Andes mountain range, and occupies a wide variety of habitats from hardpan deserts to scrublands to grasslands⁶.

Although there are several studies on the population regulation processes in mammals in general^{7,8}, and in ungulates in particular⁹⁻¹², there are very few studies in wild South American camelids that analyze population growth regulation. There have been some studies on populations of vicuña (*Vicugna vicugna*)¹³⁻¹⁵ and some on populations of guanacos¹⁶⁻¹⁸; however none of these studies considered the direct effect of density and/or climate on population growth rate.

Thus, we tested the hypothesis that population density and environmental covariates, such as average winter temperature and average annual precipitation, affect the growth rate of the guanaco population from the island of Tierra del Fuego, Chile.

Materials and methods

Study area

We analyzed the guanaco population of the "Cameron" ranch (-53.9 S, -69.3 W), with an area of the 2000 km² located in the Southern region of the Tierra del Fuego island, Chile. The altitude range is 0–300 m above sea level, and the ranch is a mosaic of

steppe and forest biomes; the latter is a deciduous forest and the steppe is composed of meadows, peats and prairies. The guanaco is the dominant herbivore, with the exception of sheep (the dominant domestic species) with densities that have fluctuated in the last decades between 11 and 23 sheep/km²⁶. Based on metabolism studies¹⁹, the guanaco/sheep equivalence factor is 1.65 (i.e., each sheep is equivalent to 0.61 guanacos), close to the values of 1.5 and 1.8 sheep per guanaco proposed by Raedeke (1978)²⁰ based on diet habits. In non-forested areas (the Patagonian steppe) the climate is characterized by an average annual precipitation of 200–400 mm, while in the forested areas the average precipitation fluctuates between 400–600 mm per year²⁰. The average annual temperature is 6.5°C and the average winter temperature is 2.2°C.

Guanaco population sampling

Guanacos were counted for 34 consecutive years between 1977 and 2012 (except 1986 and 1996), using the transect method with a variable width, and a maximum of 1000 m to each side of the transect from 1977 to 2000, and with a fixed width band from 2001 to 2012 (the latter with a maximum of 500 m to each side of the transect)²¹⁻²⁵. The sampling period was carried out in the autumn and lasted approximately 7 days between 10:30 and 19:00 h, with two observers in two 4x4 vehicles going over the main, secondary and local roads at a maximum speed of 40 km/h. Each road was covered only once, and in addition to individual guanaco counts, the following were recorded: weather conditions, time, distance (km) from the starting point, GPS coordinates, observation distance from the transect (m), an estimate of the angle to the animal's position, and – when the animals were observed in groups – the number of individuals, the type of social group, and its structure (sex, and the age class: newborn, juvenile and adult). Observations were done with model Trophy of Bushnell® 10x42 binoculars, and the GPS was a Garmin model eTrex Vista. Observation distances were made by naked eye, but the four observers had been trained in this technique using laser telemeters, GPS and the vehicles' odometers to calibrate the estimated distances. The road network and all geo-referenced observations were processed with the Arc View 9.3 Geographical Information System (SIG), and transferred using program Map Source®. The cartography was kindly provided by the Chilean "Servicio Agrícola y Ganadero" (SAG).

The population size was estimated as given in Soto²⁶ which was based in the method described by Raedeke (1978)²⁰, given by:

$$N = \frac{A * n}{2 * y * x} \quad (1)$$

where N is the total population to be estimated, A is the total study area, n is the total number of animals counted, x is the total transect distance covered (m) rounded to one meter, and y is the average of the perpendicular distance (m) 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) was estimated by (2), with $p = n/N$, and used to estimate the 95% upper and lower confidence intervals.

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

Environmental covariates

In addition to the direct density-dependence, we evaluated the possible impact of two environmental covariates on guanaco population dynamics: average annual precipitation and winter temperature (as the average of months of June, July and August). We used the 25 years (1977–2002) precipitation and temperature time series of the CRU TS 2.1 database, compiled by the Tyndall Centre, Climatic Research Unit, School of Environmental Sciences of the University of East Anglia, United Kingdom (<http://www.cru.uea.ac.uk/cru/data/hrg.htm>). As the CRU TS 2.1 data ended in 2002, we completed that time series for 2003 to 2012 from the closest meteorological station to the Cameron ranch: Punta Arenas (Chile); this data was downloaded from the Internet site of the Meteorological Service of Chile (<http://www.meteochile.gob.cl/>).

Population analysis

We estimated the population growth rate (as measured by the finite net rate of increase, λ) for each of the 36 years of the guanaco data (though population values were not available for years 1986 and 1996, and were linearly interpolated) by fitting a three age-class (newborns, juveniles and adults) matrix model to the field population estimates; as the transition matrix is a female only matrix we summed the three age classes and multiplied by two (in this population there is a 50% sex-ratio) to carry out the fit with the total field population. The fit was carried out in an Excel® spreadsheet using the Solver tool, and the sum of squares (SSQ) goodness of fit criterion was used (details can be found in Rabinovich and Zubillaga, 2012²⁷); this process resulted in a set of 36 population stage-structured matrices. From each matrix we calculated the largest positive eigenvalue²⁸ as an estimate of λ ; with the PopTools add-in, an Excel program developed by Greg Hood (<http://www.cse.csiro.au/poptools/>).

We checked the relationship between the population growth rate (as measured by the finite net rate of increase, λ) and population size (in units of natural logs) and/or climate using a stepwise regression analysis with λ as dependent variable, and total guanaco population (in natural logs), annual mean precipitation (mm/year), and winter mean temperature (°C) as independent variables. For the climatic covariates we also evaluated the effect of time lags (T), with T = 1 to 7 years for precipitation, and T = 1 year for winter

temperature; the lags were applied by averaging the previous T lagged years, as suggested by Shaw *et al.* (2012)¹⁴. These regressions were carried out using the statistical package *Statistica* (StatSoft, 2009; <http://www.statsoft.com/>). Since it is necessary to corroborate that there is no collinearity (significant correlations among the predictor variables) for multiple regressions analysis, we carried out correlation analysis between independent variables before the stepwise analysis. A *p* value < 0.05 was considered significant.

Results

The table in **Supplementary Table 1** shows the guanaco abundance data for the 36 years of sampling, the estimated values of the population rate of growth (λ) from the 36 population transition matrices, and the values of climatic variables used in the regression analysis.

The precipitation covariates with 1 to 7 year lags showed a statistically significant Pearson's correlation coefficient ($p < 0.05$), while the other independent variables didn't show a statistically significant correlation. Thus, for the stepwise analyses we chose one of these correlated covariates (precipitation with lag T = 4). The results indicated that the total population (LnNtot) was the only statistically significant variable (**Table 1**), and the model was statistically significant ($p < 0.030$ and $F_{(5, 30)} = 2.885$). **Table 1** shows both the standardized and the raw regression coefficients, with their corresponding standard errors. The magnitude of these standardized regression coefficients allows comparison of the relative contribution of each independent variable in the prediction of the dependent variable.

We carried out another regression analysis using λ as the dependent variable and only population size (in natural logs, LnNtot) as an independent variable, in order to compare it with the full model (population size and climatic covariates as independent variables). **Table 2** shows the result of this second regression analysis, which was highly significant ($p < 0.0018$, $r = 0.502$); the regression equation was $\lambda = 1.6373 - 0.0552 (\pm 0.0163) \text{ LnNtot}$; a comparison of both regressions using a two-way ANOVA test indicated that there was no statistical significant differences between them ($F = 0.803$, $p = 0.5329$).

The negative slope is an indication of a density-dependent process, since when the population increases the per capita population

Table 1. Results of stepwise regression analysis between the population growth rate (λ) as dependent variable, and (in log scale) total guanaco population (LnNtot), annual mean precipitation (Annual Precip), mean precipitation with lags of 4 years (A.Precip (T = 4)), winter mean temperature (Winter Temp.), and winter mean temperature with 1 year of lag (W.Temp (T = 1)) as independent variables. The results show the standardized regression coefficients (Sz. Reg. coeff.), their standard errors (Std.E. SRC), the raw regression coefficients (Reg. Coeff.), their standard errors (Std.E. RC) and t-test values (t-stud.).

	Sz.Reg. coeff.	Std.E. SRC	Reg. Coeff.	Std.E. of RC	t-stud.(30)	p-value
Intercept	-	-	1.5115	0.2009	7.5252	0.0000
LnNtot	-0.4408	0.1932	-0.0484	0.0212	-2.2811	0.0298
Annual precip	-0.0600	0.1611	-0.0001	0.0002	-0.3724	0.7122
Winter temp	0.1494	0.1664	0.0170	0.0190	0.8980	0.3763
A.Precip (T = 4)	-0.0139	0.1932	0.0000	0.0005	-0.0720	0.9431
W.Temp (T = 1)	0.2733	0.1596	0.0311	0.0182	1.7128	0.0971

Table 2. Regression analysis between the population growth rate (λ) as dependent variable, and (in log scale) total guanaco population (LnNtot). Interpretation of the statistical parameters as in Table 1. The results show the standardized regression coefficients (Sz. Reg. coeff.), their standard errors (Std.E. SRC), the raw regression coefficients (Reg. Coeff.), their standard errors (Std.E. RC), and t-test values (t-stud.).

	Sz.Reg. coeff.	Std.E. SRC	Reg. Coeff.	Std.E. of RC	t-stud.(30)	p-value
Intercept	-	-	1.6373	0.1624	10.0825	9.45E-12
LnNtot	-0.5024	0.1483	-0.0552	0.0163	-3.3879	0.00179

growth rate decreases (Figure 1). The intercept of the regression line at $\lambda = 1$ (population at equilibrium) results in a population size of 103,000 guanacos (51 guanaco/km²), which can be considered as an estimate of the carrying capacity of the Cameron ranch for this guanaco population.

Time series data of a guanaco population in southern Tierra del Fuego (1977–2012)

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.813321>

Discussion

We were not able to confirm the expected effect of climatic covariates on the population rate of growth in the guanaco population of the Cameron ranch. We expected such an effect because Sarno *et al.* (1999)¹⁸ found a relationship between winter weather and guanaco yearling's survival, and Rey *et al.* (2012)²⁹ recorded an effect of drought on guanaco fecundity. Thus we anticipated that as winter temperature and/or annual precipitation decrease, the population growth rate should also decrease. Our negative results are even more surprising because in the last 10–12 years the guanaco population fluctuated remarkably, suggesting some sort of interaction between population density and climatic covariates. It is well

Figure 1. Effect of population size on population growth rate (λ). On the x-axis the guanaco population from the Cameron ranch (Tierra del Fuego, Chile) is given in a natural logarithmic scale. The values of λ represent the finite population growth rate.

known that environmental effects are more important when the population size is near the carrying capacity, particularly in large mammals (as the guanaco) characterized by low reproductive rates, long life-spans, and populations that are resource-limited (features typical of species referred to as the “*K-selected*” species)³⁰. The difference between our results and that of Sarno *et al.* (1999)¹⁸ may reflect that these authors used the average winter snowfall while we considered average winter temperature.

Taper & Gogan (2002)³¹ carried out a study with the Yellowstone elk similar to our analysis, although the weather variables were included as covariates within a dynamic model (exponential, Ricker and Gompertz models). They found that spring precipitation had a positive regression coefficient, a result opposite to our conclusion for the guanaco population.

Our conclusion is that in order to test the effects of climatic covariates on population regulation of large ungulates, the use of a population dynamic model is recommended, for they may be more sensitive to the interaction between density-dependent processes and weather variables, than a simple regression between them and population growth rate. For example, our negative results do not conform to what was obtained by Shaw *et al.* (2012)¹⁴ with respect to a very phylogenetically related camelid species: the vicuña.

Using a logistic model fitted to 31 years of data these authors found that rainfall had a highly significant effect on population size with a time lag of 4 years, while in our guanaco regression analysis, no climatic covariate was statistically significant.

We conclude that, opposite to what we expected based on the bibliography of ungulate’s population dynamics, weather variables do not seem to influence the density-dependent population growth rate process.

Author contributions

MZ and JER conceived the study. NSV and OSR sampled and estimated the population size. MZ designed the analysis. MZ and JER were responsible for all writing phases of the manuscript. All authors were involved in the revision of the draft manuscript and have agreed to publish the article.

Competing interests

No competing interests were disclosed.

Grant information

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Supplementary table

Table S1. Guanaco population abundance (in units of individuals), its lower and upper limits of the 95% confidence intervals (CI), the estimated population annual rate of growth (λ), average annual precipitation (P; mm/year), and average winter temperature ($T^{\circ}w$; °C). Population values were not available for years 1986 and 1996, and were linearly interpolated.

Year	Population size	95% lower limit CI	95% upper limit CI	λ	P	$T^{\circ}w$
1977	5372	5176	5568	1.155	319.8	1.57
1978	5744	5541	5947	1.159	358.5	2.5
1979	6940	6337	7543	1.161	346.4	3
1980	6693	6128	7258	1.159	333.4	2.13
1981	8297	7707	8887	1.158	399	2.67
1982	12334	11539	13129	1.155	320.8	1.5
1983	10670	9969	11371	1.155	285.5	2.87
1984	19078	18964	19192	1.121	319	1.03
1985	11219	10501	11937	1.105	341.6	3.1
1986 *	11771	11031	12510	1.093	388.8	2.3
1987	12323	11562	13084	1.084	344.9	2.37
1988	13027	12265	13789	1.081	306.4	2.6
1989	14094	13253	14935	1.08	398.7	2.7
1990	14604	13775	15433	1.082	517.8	2.47
1991	17775	17155	18395	1.053	383.2	1.73
1992	20774	20219	21329	1.004	327.1	1.3
1993	16410	15560	17260	1.039	370	2.47
1994	17626	16716	18536	1.066	457.9	2.23
1995	21445	20153	22737	1.057	389.1	0.37
1996 *	21111	19752	22470	1.084	404.3	2.97
1997	20777	19351	22203	1.14	408	2.03
1998	28978	27749	30207	1.085	455.8	3.77
1999	27809	26518	29100	1.114	300.9	2.27
2000	28935	27446	30424	1.154	441.3	2.07
2001	38841	37366	40316	1.031	349.1	2.1
2002	38363	36810	39916	1.037	397.5	1.7
2003	32273	30818	33728	1.156	440.7	3
2004	43128	41089	45166	1.176	362.2	2.9
2005	58597	56134	61060	0.932	374	1.43
2006	52456	49820	55092	0.901	413	2.2
2007	33125	31360	34890	1.192	383.7	2.2
2008	61334	58546	64123	1.067	350.1	1.43
2009	60488	57672	63304	0.84	351.1	2.67
2010	44773	42537	47010	1.153	315.1	1.4
2011	56973	54410	59537	1.07	391.9	1.8
2012	40548	38266	42830	1.086	296	2.1

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The authors explore the population dynamics of a long-term monitored guanaco population (36 years) in the Chilean Tierra del Fuego, trying to discern if the process is governed by population size and/or environmental (climatic) variables, assuming that guanaco growth rate follows a density-dependent process. Although the topic is very interesting, the authors have room to improve the manuscript. Below the authors will find major and minor comments.

Major comments

The manuscript is classified as a "Research article" when indeed it seems a "Short note". It would greatly benefit from deeper and more detailed explanations of:

1. The theory of ungulate population dynamics, driven by density-dependent and density-independent processes; please expand this topic in the introduction and discuss more deeply your results considering the theoretical framework (see comments below).
2. The census methodology (see comments below).
3. Statistical modeling (see comments below).

Ungulate populations are regulated via endogenous forces (density-dependent processes), and exogenous forces (density-independent): weather and predation. Weather determines the primary production, i.e. the resource (forage) availability, which in turn determines the carrying capacity. On the other hand weather, through extreme conditions (e.g. severe winter climate), modulates population dynamics (starvation, survival). Predation is considered an important force which shapes population dynamics as well. In addition, poaching or overhunting act as predation, and competition with other ungulates is another important exogenous force. With this framework authors should justify:

1. The background supporting the study, as it currently is a bit poor, in my view. The authors should explain more in detail, for example, which are the differences between the density-stabilizing and the density-limiting processes, or the evidence of including climatic variables when modelling population growth rate trends.

2. The use of these climatic variables: the average annual precipitation and winter temperature. Without any justification, authors could have also included others variables in the models, as climatic variables do not account for the pattern described, but this doesn't necessarily mean that climate hasn't got any effect on the guanaco population growth rate. Moreover authors should explain if these two climatic variables are selected as indicators of primary production and harsh weather conditions.
3. As authors stated in introduction, guanaco populations have undergone overhunting (poaching) and competition with sheep, these being two of the major forces of their dramatic decline in the last century. For that reason, it is quite surprising that no variables related to livestock were included in the modelling procedure. The population has increased a lot in the studied period (x8) and just climate and/or density-dependent process do not explain alone such increase in my view. Therefore authors should consider including livestock effects, its influence on resource availability along the studied period and the mentioned overhunting, as this could really explain the detected trend.

The guanaco sampling method has changed during the studied period (different band widths). Besides, were the transects chosen based on the topography and vegetation cover of the ranch to ensure that all areas were visible to census-takers along their transects? I am not sure if that could be a source of error, but authors should discuss this point. Moreover, I recommend authors to re-analyze their data using the DISTANCE program (Buckland *et al.*, 2004) to estimate population size over the period, as the analyses performed by this package seems much more robust than the one employed by authors. If they do so, authors could also include topographic variables in the models to see whether the resulting models change. The reason is that the authors do not explain if guanacos occur in both biomes (steppe and forest), because if that was true, detection of guanacos was completely different in both ecosystems. Therefore the band width of 500 or 1000m is not valid for forests.

Regarding the population size estimated along the 36 years (Supplementary table), important (huge) differences are found, for example between 2004 and 2005 or between 2006 and 2007, or between 2007 and 2008. My concern is if such "jumps" could be related to the census surveyed. Please discuss this point.

The analytical approach employed by the authors doesn't seem appropriate in my view, as they also recognize in the discussion, and that could be the reason for not finding any climatic variable significant in the model:

1. The authors use a stepwise regression when other approaches such as logistic regressions, Ricker or Beverton-Holt models could give more suitable results. Please explain or justify your decision.
2. The selection of the best model among the candidates should be done by Akaike's information.

Minor comments

1. Refer to climatic variables or climatic effects, instead of climatic covariables.
2. Explain more in detail Corani & Gatto's studies.
3. Please remove information related to metabolic studies between guanacos and sheep (1st

paragraph of study area section).

4. Please add *Nothofagus* spp among the brackets after deciduous forest (study area section) if it is the case.
5. Give more information about livestock ranching, density, and size and the relation of livestock rangers with guanacos along the studied period (study area section).
6. Are the guanacos found both in the steppe and the forest biomes?
7. Please re-write the paragraph related to guanaco sampling through transect method in the consecutive periods (it is not clear enough).
8. Please remove information related to binoculars and GPS brands (did the authors use the same gadgets across 36 years?).
9. Explain the interest of using time lags (T) as covariables in the model.
10. Please add the Statistica version employed.
11. Please move explanations of the analyses perform from results to material & methods section.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Author Response 14 May 2014

Maria Zubillaga, Universidad Nacional de La Plata, La Plata, Argentina

- *"The background supporting the study, as it currently is a bit poor, in my view. The authors should explain more in detail, for example, which are the differences between the density-stabilizing and the density-limiting processes, or the evidence of including climatic variables when modelling population growth rate trends."*

After the following paragraph that was already in the original text:

"No population of any species can grow indefinitely, and population checks based upon different processes restrict population size and/or geographic distribution; these processes are either density-stabilizing or density-limiting"

We added the following paragraph explaining the differences between the density-stabilizing and the density-limiting processes.

"The former are of a biotic nature and depends on the interaction between individuals of the same or different species, while the latter are independent of population size. Stabilization results

from density-dependence, with a regulatory effect that varies in intensity with the size or density of the population itself, however, not all density-dependent factors are density-stabilizing. The density-limiting factors can also be considered density-responsive because the per capita amount or availability of resources decreases as the population density increases. Thus, these two types of factors (density-stabilizing and density-limiting) rarely act independently: the density-limiting factors (generally of a physical and/or climatic nature), may determine the level at which populations become stabilized by the density-dependent processes, but they do not have a stabilizing capacity per se; for this reason many wildlife population dynamic and management models include the effects of climatic variables (e.g., Dennis & Otten, 2000; Colchero et al., 2009)^{3,4}.

- *"The use of these climatic variables: the average annual precipitation and winter temperature. Without any justification, authors could have also included others variables in the models, as climatic variables do not account for the pattern described, but this doesn't necessarily mean that climate hasn't got any effect on the guanaco population growth rate. Moreover authors should explain if these two climatic variables are selected as indicators of primary production and harsh weather conditions."*

To explain and justify the use of these climatic variables the paragraph below was incorporated in the section "Climatic variables":

"These climatic variables were selected because some studies suggested that they have influence on guanaco demographic parameters: Rey et al. 2012²⁶ observed that after a severe drought the proportion guanaco yearlings/female decreased significantly, and Sarno et al. 1999¹⁷ detected a negative effect of winter snowfall on guanaco juvenile survival; because we had insufficient snowfall data we used the winter temperature as a proxy for winter snowfall."

- *"As authors stated in introduction, guanaco populations have undergone overhunting (poaching) and competition with sheep, these being two of the major forces of their dramatic decline in the last century. For that reason, it is quite surprising that no variables related to livestock were included in the modelling procedure. The population has increased a lot in the studied period (x8) and just climate and/or density-dependent process do not explain alone such increase in my view. Therefore authors should consider including livestock effects, its influence on resource availability along the studied period and the mentioned overhunting, as this could really explain the detected trend."*

In relation with the "poaching" the following paragraph was incorporated in section "Study area" to justify why this variable was not considered in our study:

"In contrast to the continent, the puma (Puma concolor), the main predator of guanacos, is absent in the island; since 1977 the guanaco hunting has been controlled by Chilean National Forest Corporation (CONAF, according to its Spanish acronym) and the Chilean Agricultural and Livestock Service (SAG, according to its Spanish acronym)."

In relation to the suggestion to incorporate livestock in the analysis, we re-analyzed our multiple regression incorporating the variable livestock as sheep

population. We re-processed the regressions incorporating the sheep population as a new independent variable as a possible predictor of the guanaco population growth rate (I); so our new analysis increased from 5 to 6 independent variables: sheep population, guanaco population size, winter temperature, winter temperature with a lag of 1 year, annual precipitation, annual precipitation with a lag of 3 years. Our main results didn't change and it was confirmed that only the guanaco population size seems to have an effect on the population growth rate (I). These changes can be found in the "Methods" and in the "Results" sections.

- *"The guanaco sampling method has changed during the studied period (different band widths). Besides, were the transects chosen based on the topography and vegetation cover of the ranch to ensure that all areas were visible to census-takers along their transects? I am not sure if that could be a source of error, but authors should discuss this point."*

In the Section "Guanaco population sampling" we added the following paragraphs where we explain the motive of the change and justify the transects chosen:

"The sampling methodology was changed by an expert recommendation made in 1995²³; as in year 2000 the fixed and the undefined band width methods were applied simultaneously, we tested both results and found no significant statistical difference between them."

"Despite randomly selected transects are recommended²⁴, preexisting roads were used because according to Soto (2010)¹⁸ the existing system of roads is an adequate sample of the area."

- *"Moreover, I recommend authors to re-analyze their data using the DISTANCE program (Buckland et al., 2004) to estimate population size over the period, as the analyses performed by this package seems much more robust than the one employed by authors. If they do so, authors could also include topographic variables in the models to see whether the resulting models change. The reason is that the authors do not explain if guanacos occur in both biomes (steppe and forest), because if that was true, detection of guanacos was completely different in both ecosystems. Therefore the band width of 500 or 1000m is not valid for forests."*

In the Section "Guanaco population sampling" the following paragraphs were incorporated to justify the methodology used:

"Raedeke (1978)¹⁹ claims that the Leopold method is valid when the following conditions are satisfied: (1) the road systems must be an adequate sampling of the study area, (2) the network road must be randomly distributed, and (3) the animals included in the sampling must be randomly distributed in relation to the observer's route; and he considers that in the south of the Tierra del Fuego Island these assumptions are fulfilled. Soto 2010¹⁸ compared population estimations by the Leopold and Distance methods and found that the value of the means estimate by Leopold methods fall within the confidence intervals estimated by Distance; additionally, as all sampling periods used the same methodology whatever bias might exist in the estimation of the mean abundance using the Leopold method, the relative changes among years (and thus the temporal trend) will be adequately represented; thus, we conclude that the Leopold's method seems adequate for our purposes¹⁸."

In relation to the forest and the sampling methodology, as the area occupied by forests is low and it has some degree of intervention, the visibility of the guanaco is adequate, hence we considered that the forest is a minor component and that does not affect the efficiency of the sampling procedure. In the section "Study area" the next paragraph was incorporated:

"The forested area is about 8.8% of the total study area, with different degrees of forest clearance that offers adequate visibility for guanaco sampling."

- *"Regarding the population size estimated along the 36 years (Supplementary table), important (huge) differences are found, for example between 2004 and 2005 or between 2006 and 2007, or between 2007 and 2008. My concern is if such "jumps" could be related to the census surveyed. Please discuss this point."*

In the "Discussion" section we added the following discussion as required by the reviewer:

"The results of the guanaco population sampling suggest a certain trend in the population size, with a sort of exponential growth in the first few years, becoming more variable as the population grows, with more marked fluctuations during the last 10-12 years; this may imply that the population is becoming stabilized, possibly approaching its carrying capacity. On the other hand, the sampling results of those last 10-12 years show abrupt "jumps" in some years (for example 2004-2005) that may be the consequence of the mobility of guanacos from the Cameron ranch to neighboring sites and vice versa; since the transect sampling does not identify individuals the effects of possible local displacements could not be considered."

- *"The authors used a stepwise regression when other approaches such as logistic regressions, Ricker or Beverton-Holt models could give more suitable results. Please explain or justify your decision."*

Our goal was to carry out a preliminary analysis that would guide us in the study of the population regulation process in the guanaco. As there are studies in ungulate that have used simple multiple regression analysis and obtained good/satisfactory results, we considered that it was of interest to test this technique as a first step in such an analysis.

In the manuscript the following paragraph was incorporated in the "Discussion" section to justify our decision:

"Contrary to what was expected based on the bibliography of ungulate's population dynamics, weather variables do not seem to influence the density-dependent population growth rate process of the guanaco population of the Cameron ranch. Our aim was to carry out a preliminary analysis that would help identify some of the regulation processes in guanaco population; so we used a simple multiple regression analysis as a first step in that direction; nevertheless, our conclusion is that in order to test the effects of climatic variables on population regulation of large ungulates as the guanaco, the use of a

population dynamic model would be recommended, for they seem to account better for the interaction between density-dependent processes and weather variables than a simple regression between the latter and guanaco population growth rate."

- *"The selection of the best model among the candidates should be done by Akaike's information"*

This suggestion was considered and the respective Akaike's values were calculated.

Minor comments:

1. *"Refer to climatic variables or climatic effects, instead of climatic covariables."*

The recommendation was applied.

2. *"Explain more in detail Corani & Gatto's studies."*

With the previous changes we realize that the citation of Corani and Gatto (2007) is not necessary any more. Mainly because the essence of that paper is the proposal of a methodology that is not strictly relevant to our work. The phrase with this citation was deleted.

3. *"Please remove information related to metabolic studies between guanacos and sheep (1st paragraph of study area section)."*

The suggestion was carried out.

4. *"Please add Nothofagus spp among the brackets after deciduous forest (study area section) if it is the case."*

This information is already incorporated.

5. *"Give more information about livestock ranching, density, and size and the relation of livestock rangers with guanacos along the studied period (study area section)."*

This information was already incorporate in the section "Sheep population"

6. *"Are the guanacos found both in the steppe and the forest biomes?"*

Yes, the guanacos use both biomes, but they mostly use the open habitat (i.e. steppes and meadows).

7. *"Please re-write the paragraph related to guanaco sampling through transect method in the consecutive periods (it is not clear enough)."*

The paragraph was improved.

8. *"Please remove information related to binoculars and GPS brands (did the authors use the*

same gadgets across 36 years?)."

The recommendation was carried out.

9. "Explain the interest of using time lags (T) as covariables in the model."

The next paragraph was incorporated in section "Population analysis":

"The inclusion of time lags is convenient because it may detect possible cumulative climatic effects on ungulate population growth rates as it was observed in, e.g., deer and moose²⁹ and in vicuñas¹³".

10. "Please add the Statistica version employed."

The *Statistica* tools was replaced by language **R** (Version 0.97.449 – ©2009-2012 RStudio, Inc.) to obtain the value of Akaike and satisfy the item 3.2 (see above).

11. "Please move explanations of the analyses perform from results to material & methods section."

The recommendation was carried out.

Competing Interests: No competing interests

Reviewer Report 20 November 2013

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Ricardo Baldi

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The authors hypothesized that population density and climatic variables affect the growth rate of the population of guanacos in the study area. However, as it is detailed under the "Study area" subsection, the domestic sheep share the area with the guanaco and substantial changes in stocking rate have been reported for the ranch during the study period. It is known that sheep and guanacos select similar diets across different parts of the range they share, and usually sheep presence and abundance explain a substantial amount of variation in the abundance of guanacos, included the study area comprising the Estancia Cameron as described by [Raedeke \(1979\)](#). In his work, Raedeke described that sheep are managed "rotationally" around the property, taken seasonally to different areas in winter and summer, and this makes guanacos move seasonally to

the forest habitat. Therefore, it would be expected that variations in sheep abundance, not only seasonally but in total numbers through time, could affect the estimates of guanaco abundance. In my opinion, this is a major issue in the design of this work. Also, as explained below, the survey design of this work could play a key role in the quality of the estimates obtained, which is reflected also in the interpretation of results. All of these do not mean that density dependent processes are not likely to occur, but to my understanding it is not possible to rule out other processes to be conclusive.

Guanaco population sampling

The surveys were conducted at a 2,000 km² ranch where the habitat is a mosaic of steppe and forest biomes. The authors indicate that they surveyed guanacos using the “transect method with a variable width” from 1977 to 2000. Is this the distance sampling? If so, it is based on measuring the perpendicular distance from the transect to the object. Also, it is says that the surveying methodology was changed to “fixed width band” in 2001 and subsequent years. Some comments and questions on these issues regarding survey design are:

1. Were both the steppe and forest habitats surveyed using the same methodology? Transect lines to observe individuals and make direct counts are commonly used in open habitats, but not in the forest. However if this was not the case, the authors need to account for the variation in the probability of detection as it is expected to vary significantly between such contrasting habitat types.
2. There was a change in the surveying method, which also brings the point of detection probability. While the line transect method assumes that the probability of detecting objects on the line (distance=0) is $p=1$, and as objects are far from the line the probability of detection follows a certain declining function, the main assumption of the strip transect method is that the probability of detecting objects within the strip is 1 (i.e. no objects are left undetected). This variation in the probability of detection according to the methodology applied during each period must be discussed. Also, the ways that the density estimates were obtained are unclear and must be specified (i.e. distance sampling, other calculation methods).
3. Regarding the estimate of population size, several considerations can be made about the extrapolation of absolute densities to population numbers. First, the spatial pattern of the transects surveyed could be determinant of biased estimates, if the objects are not randomly distributed in relation to the survey line (i.e. if the transect follows a geographic feature in such a way the animals are either attracted or deterred). Perhaps the transects are located across certain areas – for example the steppe – but not the forest and thus the estimate could be biased towards the density calculated for the surveyed portion of the total area. This is especially important at the time of extrapolate densities to obtain population size numbers, as densities are strictly valid for the areas effectively surveyed while traveling along the transect lines. In any case, it would be useful to provide the distribution of surveyed lines across the area. The second point I find relevant to discuss regarding survey design is the proportion of the area effectively surveyed. How many km² were comprised by the lines and strips surveyed? Again, the extrapolation of densities to population size at a larger scale must account for possible limitations related to the survey design and effort invested.

Results and discussion

Major fluctuations of the guanaco population occurred during the last 10-12 years analyzed, as can be found in the additional data file provided, and also pointed out by the authors. But this variation could well be due to the changes in methodology at the time of the population surveys. As said above, it is necessary to provide detailed information on the type of survey conducted, the differences with the previous method and the way the density estimates were obtained. It would be informative if the authors provide the errors associated with the population estimates.

As proposed above, sheep densities could be affecting guanaco population trends, but the design of the work does not allow accounting for this factor. In my opinion, sheep densities must be included as an explanatory variable as there is evidence they affect guanaco numbers. Also, as the authors concluded that in this study the guanaco populations was near carrying capacity, and this must be common to both guanacos and sheep, thus sheep must be considered in the analysis as its density was markedly variable during the study period. Another factor that should be considered at the time of the discussion is the possibility of guanacos moving from the surveyed surroundings or even from Cameron to neighboring sites, as they may respond to changes in the spatial availability of resources by occupying different sites. In summary, the marked fluctuations in population size require the examination and discussion of other possible factors before concluding that density dependent processes would drive population trends.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Author Response 14 May 2014

Maria Zubillaga, Universidad Nacional de La Plata, La Plata, Argentina

- *"The authors hypothesized that population density and climatic variables affect the growth rate of the population of guanacos in the study area. However, as it is detailed under the "Study area" subsection, the domestic sheep share the area with the guanaco and substantial changes in stocking rate have been reported for the ranch during the study period. It is known that sheep and guanacos select similar diets across different parts of the range they share, and usually sheep presence and abundance explain a substantial amount of variation in the abundance of guanacos, included the study area comprising the Estancia Cameron as described by Raedeke (1979). In his work, Raedeke described that sheep are managed "rotationally" around the property, taken seasonally to different areas in winter and summer, and this makes guanacos move seasonally to the forest habitat. Therefore, it would be expected that variations in sheep abundance, not only seasonally but in total numbers through time, could affect the estimates of guanaco abundance. In my opinion, this is a major issue in the design of this work. Also, as explained below, the survey design of this work could play a key role in the quality of the estimates obtained, which is reflected also in the interpretation of results. All of these do not mean that density dependent processes are not likely to occur, but to my understanding it is not possible to rule out other processes to be conclusive."*

In relation to the suggestion to incorporate livestock in the analysis, we re-analyzed our regression incorporating the variable livestock as sheep population; we re-processed the regressions incorporating the sheep population as a new independent variable of the guanaco population growth rate (I); so our new analysis increased from 5 to 6 independent variables: sheep population, guanaco population size, winter temperature, winter temperature with a lag of 1 year, annual precipitation, annual precipitation with a lag of 3 years. Our main results didn't change and it was confirmed that only the guanaco population size seems to have an effect on the population growth rate (I). These changes can be found in the "Methods" and in the "Results" paragraphs.

- *"The surveys were conducted at a 2,000 km² ranch where the habitat is a mosaic of steppe and forest biomes. The authors indicate that they surveyed guanacos using the "transect method with a variable width" from 1977 to 2000. Is this the distance sampling? If so, it is based on measuring the perpendicular distance from the transect to the object."*

No, the sampling methodology did not use the program Distance. The citations of Buckland et al. (1993 and 2001) were removed to avoid possible misinterpretations with the sampling methodology used. The method used to estimate the population size was the King method modified by Leopold (1933) as described in Raedeke (1978). In the manuscript it was explained and justified this method with the following paragraph:

"Raedeke (1978)¹⁹ claims that the Leopold method is valid when the following conditions are satisfied: (1) the road systems must be an adequate sampling of the study area, (2) the network road must be randomly distributed, and (3) the animals included in the sampling must be randomly distributed in relation to the observer's route; and he considers that in the south of the Tierra del Fuego Island these assumptions are fulfilled. Soto 2010¹⁸ compared population estimations by the Leopold and Distance methods and found that the value of the means estimate by Leopold methods fall within the confidence intervals estimated by Distance; additionally, as all sampling periods used the same methodology whatever bias might exist in the estimation of the mean abundance using the Leopold method, the relative changes among years (and thus the temporal trend) will be adequately represented; thus, we conclude that the Leopold's method seems adequate for our purposes¹⁸. The area effectively surveyed in each sampling period was around 420 km² (about 20%, of the area under study)."

- *"Also, it is says that the surveying methodology was changed to "fixed width band" in 2001 and subsequent years. Some comments and questions on these issues regarding survey design are:*
 1. *Were both the steppe and forest habitats surveyed using the same methodology? Transect lines to observe individuals and make direct counts are commonly used in open habitats, but not in the forest. However if this was not the case, the authors need to account for the variation in the probability of detection as it is expected to vary significantly between such contrasting habitat types."*

We corrected in the manuscript the years where the change in band width occurred: variable band width from 1977 to 1995, and with a fixed width band (with a maximum of 500 m to each side of the transect) from 1996 to 2012.

The area occupied by forest is low and it has some degree of intervention, the visibility of the guanaco is adequate, hence we considered that the forest is a minor component and it does not affect the efficiency of sampling. In the section "Study area" the following paragraph was incorporated:

"The forested area is about 8.8% of the total study area, with different degrees of forest clearance that offers adequate visibility for guanaco sampling."

- *"There was a change in the surveying method, which also brings the point of detection probability. While the line transect method assumes that the probability of detecting objects on the line (distance=0) is $p=1$, and as objects are far from the line the probability of detection follows a certain declining function, the main assumption of the strip transect method is that the probability of detecting objects within the strip is 1 (i.e. no objects are left undetected). This variation in the probability of detection according to the methodology applied during each period must be discussed. Also, the ways that the density estimates were obtained are unclear and must be specified (i.e. distance sampling, other calculation methods)."*

We improved this section and the next paragraph was incorporate to explain this change. The population size was estimated by King method modified by Leopold (1933) as described by Raedeke (1978), which was also clarified in the manuscript.

"The sampling methodology was changed by an expert recommendation made in 1995²³; as in year 2000 the fixed and the undefined band width methods were applied simultaneously, we tested both results and found no significant statistical difference between them."

- *"Regarding the estimate of population size, several considerations can be made about the extrapolation of absolute densities to population numbers. First, the spatial pattern of the transects surveyed could be determinant of biased estimates, if the objects are not randomly distributed in relation to the survey line (i.e. if the transect follows a geographic feature in such a way the animals are either attracted or deterred). Perhaps the transects are located across certain areas – for example the steppe – but not the forest and thus the estimate could be biased towards the density calculated for the surveyed portion of the total area. This is especially important at the time of extrapolate densities to obtain population size numbers, as densities are strictly valid for the areas effectively surveyed while traveling along the transect lines. In any case, it would be useful to provide the distribution of surveyed lines across the area. The second point I find relevant to discuss regarding survey design is the proportion of the area effectively surveyed. How many km² were comprised by the lines and strips surveyed? Again, the extrapolation of densities to population size at a larger scale must account for possible limitations related to the survey design and effort invested."*

Although the transects are not randomly distributed, the preexisting roads can be considered as an adequate sample of the area. This comment was incorporate in the manuscript.

"Despite randomly selected transects are recommended²⁴, preexisting roads were used because according to Soto (2010)¹⁸ the existing system of roads is an adequate sample of the area."

- The second point was considered and the area effectively surveyed was estimated. In the "Guanaco population sampling" section the following paragraph was incorporated:

"The area effectively surveyed in each sampling period was around 420 km² (about 20%, of the area under study)."

- *"Major fluctuations of the guanaco population occurred during the last 10-12 years analyzed, as can be found in the additional data file provided, and also pointed out by the authors. But this variation could well be due to the changes in methodology at the time of the population surveys. As said above, it is necessary to provide detailed information on the type of survey conducted, the differences with the previous method and the way the density estimates were obtained. It would be informative if the authors provide the errors associated with the population estimates."*

The errors associated with the population estimates are given in Table S1 where the lower and upper limits of the 95% confidence intervals (CI) are shown.

- *"As proposed above, sheep densities could be affecting guanaco population trends, but the design of the work does not allow accounting for this factor. In my opinion, sheep densities must be included as an explanatory variable as there is evidence they affect guanaco numbers. Also, as the authors concluded that in this study the guanaco populations was near carrying capacity, and this must be common to both guanacos and sheep, thus sheep must be considered in the analysis as its density was markedly variable during the study period. Another factor that should be considered at the time of the discussion is the possibility of guanacos moving from the surveyed surroundings or even from Cameron to neighboring sites, as they may respond to changes in the spatial availability of resources by occupying different sites. In summary, the marked fluctuations in population size require the examination and discussion of other possible factors before concluding that density dependent processes would drive population trends."*

This factor (sheep population) has been incorporated, and the corresponding analysis was carried out; see in the "Materials and methods" section "Sheep Population" and the section "Results". In the "Discussion" section the following paragraph was included where we recognized the possibility of guanaco moving as possible source of error in the sampling:

"The results of the guanaco population sampling suggest a certain trend in the population size, with a sort of exponential growth in the first few years, becoming more variable as the population grows, with more marked fluctuations during the last 10-12 years; this may imply that the population is becoming stabilized, possibly approaching its carrying capacity. On the other hand, the sampling results of those last 10-12 years show abrupt "jumps" in some years (for example 2004-2005) that may be the consequence of the mobility of guanacos from the Cameron ranch to neighboring sites and vice versa; since the transect sampling does not identify individuals the effects of possible local displacements could not be considered."

Competing Interests: None

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