Population dynamics of the vicuña (*Vicugna vicugna*): density-dependence, rainfall, and spatial distribution

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The vicuña (*Vicugna vicugna*) is a South American camelid that has been hunted to near extinction. Following the establishment of conservation programs, vicuñas have successfully recovered to their current ''Least Concern'' International Union for Conservation of Nature and Natural Resources status. We analyze a 31-year vicuña census data set from northern Chile in order to investigate the influence of various factors on vicuña population dynamics. During the first 15 years, population dynamics are driven by strong growth as the population recovers from overhunting, and during the last 15 years dynamics are dominated by fluctuations around carrying capacity. We find that the best fit of the census data is a logistic growth model that takes into account how changes in rainfall and primary productivity lead to fluctuations in carrying capacity, suggesting that the resources limiting vicuña population size are not constant but change over time. We also find that the spatial distribution of vicuñas changes over time with respect to the nutrient-rich bofedales (Andean peatlands). Our study demonstrates the importance of collecting and analyzing long-term census data, and suggests that further insight could be gained if vicuña location with respect to habitat type was recorded during the census.

Key words: carrying capacity, density-dependence, logistic model, primary productivity, rainfall, *Vicugna vicugna*, vicuña

The vicuña (*Vicugna vicugna*) is a member of the camelid family found in the altiplano or puna ecosystem of South America (Koford 1957). Excessive hunting of vicuñas for their valuable wool caused the population to decline severely, dropping from numbering in the millions during the 1500s to only thousands in the mid-1900s (Torres 1992). In 1969 Peru and Bolivia signed an agreement to each start a national vicuña conservation program, which Argentina and Chile joined in 1979 (Madariaga and Galaz 2005). These programs have been effective and vicuñas are currently classified as ''Least Concern'' on the *IUCN Red List* (International Union for Conservation of Nature and Natural Resources 2009).

In Chile, the National Forestry Service (Corporación Nacional Forestal) established Lauca National Park in the province of Parinacota in northern Chile and initiated an annual vicuña census to protect and count vicuñas in the area (Galaz 2005). According to this census data set, there are 14,455 vicuñas in Chile (as of 2007), up from 2,176 in 1975 when the census was 1st conducted. This data set is the longest running record of vicuña counts in any area, and presents a unique opportunity to examine long-term vicuña population dynamics and determine which factors influence vicuña populations.

The population dynamics of vicuñas during the first 15 years of the census were marked by steady growth as the population recovered from overhunting and approached its carrying capacity (Bonacic et al. 2002; Cattan and Glade 1989). Population numbers during the period since this recovery point were more variable and therefore likely driven by whatever factors that influence vicuña populations near carrying capacity. Because ungulate populations are thought to naturally hover at approximately their carrying capacity (McCullough 1999), we hypothesized that any fluctuations in vicuña population size during the past 15 years were due to

fluctuations in carrying capacity. An herbivore's carrying capacity is likely to depend on the amount of forage available, which in turn depends on rainfall (Coe et al. 1976; Mansson et al. 2007).

The aim of our research was to investigate the influence of various factors on vicuña population dynamics. To test for the effect of rainfall, as mediated by forage, on vicuña population sizes, we fit a number of models to the vicuña data, both with and without a rainfall-dependence. We found that a rainfall-dependent logistic model fit the vicuña census data quite well, suggesting that the resources limiting vicuña population size are not constant but change over time, and that these temporal fluctuations can be mostly explained by fluctuations in rainfall. We also looked at the effects of habitat distribution and domestic animals on the spatial patterns of vicuñas across census sectors.

MATERIALS AND METHODS

Vicuña populations were monitored by annual ground census surveys in northern Chile, starting in 1975. The census area was a region of about 5,415 km^2 within the Arica/Parinacota and Tarapacá regions in northern Chile (Fig. 1), which contains approximately 97% of all the vicuñas within Chile. This region is part of the puna, the high plains found in the Andes mountains at approximately 3,800–4,500 m above sea level. The puna is an arid grassland ecosystem characterized by extreme weather conditions: little rainfall (150–500 mm annually), low year-round temperatures (averaging 0°C in summer and −10°C in winter) with daily fluctuations of up to 25°C, and intensive solar radiation (Castellaro 2005). Because there is little rainfall outside of the December–February rainy season, the only year-round sources of water in the region are permanent wet areas (peatlands) near streams and lakes, called bofedales or vegas (Castellaro 2005; Renaudeau d'Arc et al. 2000). These areas are dominated by the plant species *Oxychloe andina* and *Werneria pygmaea*, and contribute most of the available forage in the region; a study of puna productivity found that bofedales contributed 40% of the primary productivity of the ecosystem, even though they made up only 5% of the study area (Corporación Nacional Forestal–Fundación para la Innovación Agraria 2002). Vicuñas spend most of their waking time foraging (Vilá and Cassini 1993), and much of this is spent either in bofedales or moving between these areas and their sleeping grounds (Renaudeau d'Arc et al. 2000).

A full census of vicuñas in the region was conducted each year in October by Corporación Nacional Forestal park rangers, using a standard protocol (Cattan and Glade 1989; Rodriguez and Nuñez 1987) and in compliance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). The census region was divided into 32 different sectors (Fig. 1), which were defined based on natural boundaries, such as steep slopes, rivers, and roads, and range in size from roughly 40 to 400 km^2. The ranger team, consisting of approximately 6 individuals, walked fixed
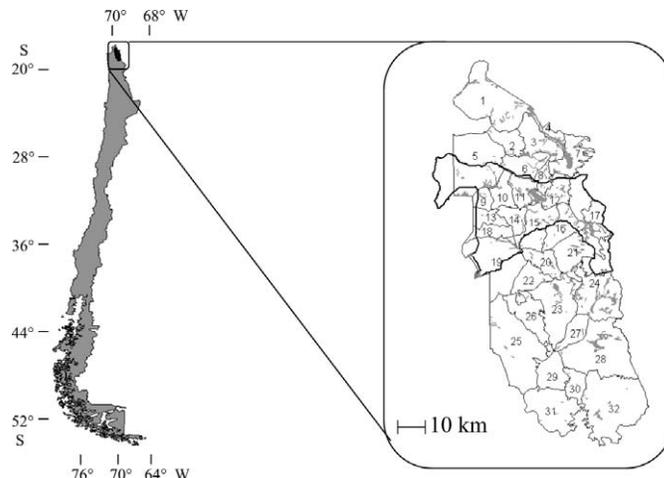

FIG. 1.—Location of the study site within Chile (left), and the 32 census sectors (right). Most of Lauca National Park (outlined in black, right) is included in the census region. The spatial distribution of bofedales, the most nutrient-rich areas, is shown in gray (right).

transects within each sector, each separated by approximately 3 km (Galaz 1998; Torres 1992). Transects were chosen based on the topography of the region to ensure that all areas were visible to census-takers along their transects. Nearby transects were walked simultaneously to minimize the number of vicuñas that were either missed or counted more than once. Rangers use binoculars to count and classify all observable vicuñas within each sector. Vicuñas were classified by type—family groups (1 male, several females, and calves), bachelor groups (bachelor males), and solitary animals (Galaz 2005). Census data were collected from 1975 to 2006, and totals were reported by sex and age class (males, females, calves, bachelor males, and solitary individuals) for each of the 32 sectors (Fig. 2). No census was conducted in 1994, 1997, 1998, or 2000, and a partial census (only half of the sectors) was conducted in 1993 and 1996, due to budgetary constraints within Corporación Nacional Forestal for those years. We omitted data from the partial census years from our analysis, instead of estimating total counts for these years, which would have led to overfitting of the model.

To determine what factors influence vicuña population dynamics, we collected data on several environmental variables. We obtained monthly rainfall data (in mm) from 10 stations across the census region. Data were available for different time periods for each station, ranging from 1961 to 2006. We calculated annual rainfall for each year t as the sum of monthly rainfall from June in year $t − 1$ through May in year t. We then calculated the annual rainfall for the region as the average annual rainfall across all stations with available data in a given year, for each year (Fig. 3). Because rainfall stations were not distributed across the entire census region, but only located in the northernmost half, we did not incorporate spatial trends in rainfall into our analysis.

To test for the importance of food-mediated effects of rainfall on carrying capacity, we fit 3 types of models (discrete logistic, Ricker, and Beverton–Holt) to the census data
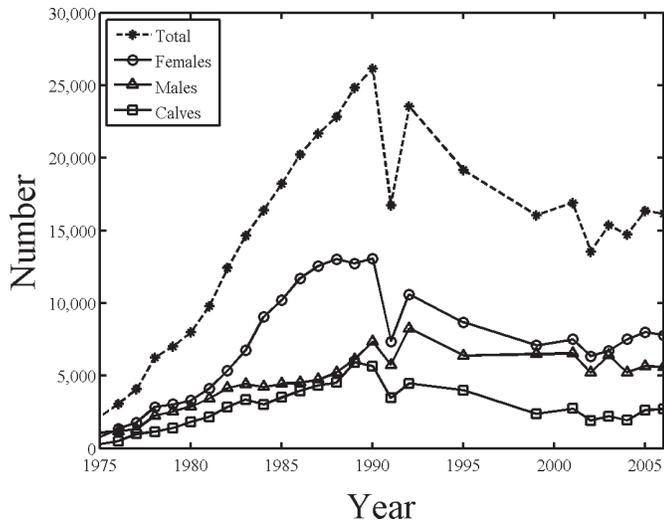
Fig. 2.—Number of censused vicuñas, pooled across all census sectors, from 1975 to 2006, both the total number of animals and by sex and age class: females, males (both bachelor and family males), and calves. Solitary animals, which made up less than 1% of the total, are not shown separately, but are included in the total counts.

(Table 1). These models were chosen because they are different discrete versions of the logistic model (the simplest model of density-dependent population growth—Pastor 2008) that have commonly been used to model density-dependent population dynamics in large mammals as well as in other species (e.g., Brook and Bradshaw 2006; Chamaille-Jammes et al. 2008; Pascual et al. 1997). For each model, we fitted 1 version with a constant carrying capacity and others with carrying capacity as a function of rainfall. The models were fitted with nonlinear least squares, using the curve-fitting toolbox in MATLAB (The Mathworks Inc., Natick, Massachusetts), which outputs sum of squares due to error (*SSE*) and r^2 as goodness-of-fit metrics. We then evaluated the fit of each model by calculating Akaike's information criterion, corrected
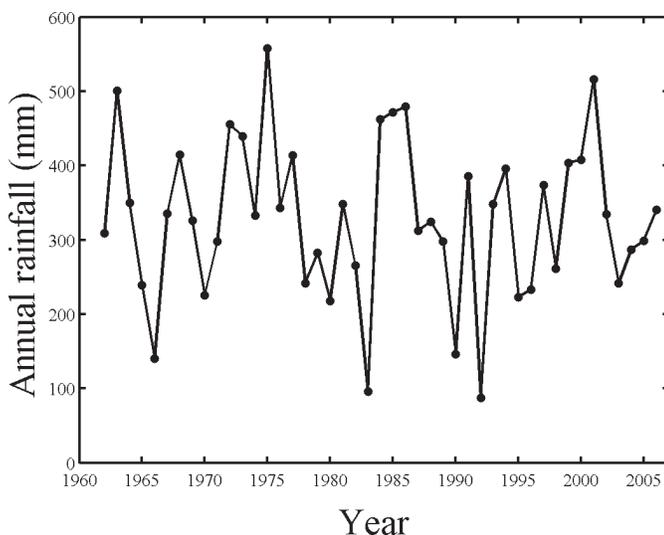

Fig. 3.—Annual rainfall (in mm), averaged across the stations for which data were available in each year.

Table 1.—List of alternative models that were fit to vicuña population size.

Model	Equation
Discrete logistic	$N(t + 1) = N(t)[1 + r(1 - N(t)/K)]$
Ricker	$N(t + 1) = N(t)\exp[r(1 - N(t)/K)]$
Beverton–Holt	$N(t + 1) = rN(t)/(1 + N(t)/K)$

for small sample size (AIC$_c$) from the *SSE* (Symonds and Moussalli 2011). In each model, $N(t)$ represents the number of vicuñas at a given time t, and K and r are fitted constants. Each of these models predicts that when the number of individuals, $N(t)$, is small (i.e., far from the carrying capacity, K), the population size should increase rapidly, with growth rate r. As the population approaches its natural carrying capacity, the rate of growth slows until it reaches zero and the population size becomes constant over time. In the rainfall-dependent versions of the models, the carrying capacity took the form:

$$K = K(t) = K_0 + \frac{\alpha}{T} \sum_{n=1}^{T} p(t - n), \qquad (1)$$

where K_0, α, and T are fitted constants and p(t) is precipitation (rainfall). Thus, the carrying capacity at each time, K(t), is the sum of a basal carrying capacity, K_0, plus some fluctuation, which is a function of the average rainfall during the previous T years. The length of time lag between changes in rainfall and changes in herbivore dynamics varies across different species and systems, but is thought to be on the order of years to decades (Caughley and Gunn 1993; Mansson et al. 2007; Ogutu and Owen-Smith 2005; Ogutu et al. 2008). Therefore, we fit the model using different time lags (values of T), ranging from 1 to 15 years (the maximum amount possible given the available rainfall data).

We also obtained data on spatial vegetation patterns within the study region, focusing on bofedales (peatlands), the most nutrient-rich areas of the puna. We mapped distribution of bofedales in the study region, using ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California; Fig.1), and calculated the total bofedal area for each census sector. Bofedales were unevenly distributed across sectors and made up between 0% and 20% of each sector's area. We hypothesized that the spatial distribution of vicuñas would be related to the distribution of bofedales because vicuñas spend much of their time foraging in these areas (Renaudeau d'Arc et al. 2000). Bofedales also serve as foraging grounds for the domestic animals in the region, and therefore likely influence their distribution as well. To explore the spatial patterns of both vicuñas and domestic animals (mainly llamas and alpacas), we calculated the correlation between the average number of each animal type and the bofedal area in each sector. Although the location of bofedales is unlikely to change over timescales of several decades, the size of bofedales could potentially vary from year to year. However, because we only had size estimates for a single year, we did not incorporate bofedal area into our temporal analysis of the vicuña data. To explore the temporal pattern of vicuña distribution with respect to bofedales

TABLE 2.—Estimates of the parameters T (in years), K_0 (in individuals), α, and r; the number of variables (k); Akaike information criterion, corrected for small sample size (AIC_c) scores; differences in AIC_c scores between each model and the top-ranked model (ΔAIC_c); and r^2 values. Shown are the results for all 3 model types with constant carrying capacity, and the rainfall-dependent models with ΔAIC_c values less than 6.

Model	T	K_0	α	r	k	AIC_c	ΔAIC_c	r^2
Constant carrying capacity models								
Logistic	—	18,930	—	0.5157	2	406.26	8.07	0.75
Ricker	—	18,940	—	0.4495	2	406.72	8.53	0.75
Beverton–Holt	—	29,390	—	1.645	2	407.36	9.17	0.74
Rainfall-dependent carrying capacity models								
Logistic	2	8,000	37.48	0.5013	4	403.82	5.64	0.82
Logistic	3	8,000	36.84	0.5095	4	401.66	3.48	0.83
Logistic	4	8,000	36.76	0.5189	4	398.19	0.00	0.85
Logistic	5	8,000	36.52	0.5191	4	399.38	1.19	0.85
Logistic	6	8,000	36.36	0.5151	4	400.96	2.78	0.84
Logistic	7	8,000	36.20	0.5094	4	403.07	4.89	0.82
Ricker	2	8,000	37.30	0.4431	4	403.39	5.21	0.82
Ricker	3	8,000	36.81	0.4478	4	401.60	3.41	0.83
Ricker	4	8,000	36.75	0.4515	4	399.26	1.07	0.85
Ricker	5	8,000	36.53	0.4497	4	400.85	2.67	0.84
Ricker	6	8,000	36.35	0.4458	4	402.60	4.42	0.83
Beverton–Holt	2	8,000	75.96	1.627	4	402.35	4.17	0.83
Beverton–Holt	3	8,000	74.49	1.629	4	400.38	2.20	0.84
Beverton–Holt	4	8,043	74.44	1.628	4	398.29	0.10	0.85
Beverton–Holt	5	8,000	75.00	1.622	4	400.46	2.27	0.84
Beverton–Holt	6	8,000	75.96	1.613	4	402.61	4.42	0.83

locations, we plotted the fraction of the vicuña population in the ''highest quality'' sectors (those with the most bofedales) over time. There appeared to be a clear shift in the fraction of vicuñas in these sectors around 1991, so we tested for a difference using the nonparametric Mann–Whitney U-test.

Data on the number of domestic animals present in the study region were obtained from the Agricultural and Livestock Service (Servicio Agrícola y Ganadero) in Chile. In 2000, Servicio Agrícola y Ganadero started requiring annual self-reported declaration of the number and type of livestock in each household. We used ArcView to group the data by corresponding vicuña census sectors based on approximate location. To determine the spatial distribution of domestic animals we calculated the number in each sector averaged across the years for which data were available (2000–2001 and 2003–2006). To facilitate the comparison with domestic animals, we averaged the number of vicuñas in each sector across the same time period, when looking at the relationship with bofedal area. Because long-term temporal counts of domestic animals were not available, we did not incorporate domestic animals into our temporal analysis of the vicuña data.

Other potential factors that could influence vicuña population dynamics are predation by pumas (Donadio et al. 2010) and mortality by disease (Galaz 2005). However, because there are no data on how either of these factors affect vicuña populations in the study area, these were not included in our analysis.

RESULTS

All 3 types of models (discrete logistic, Ricker, and Beverton–Holt) generally provided equally good fits to the vicuña census data. The best fit (lowest AIC_c score) version of each model type was one with a rainfall-dependent carrying capacity, with a dependence on rainfall over the past 4 years (T = 4; Table 2). The constant carrying capacity versions of all 3 models had a much poorer fit, indicated by higher AIC_c scores. For example, the constant carrying capacity discrete logistic model matched the data well from 1975 to 1985, but failed to capture the continued rise in vicuña population during the late 1980s, and the drop during the 1990s (Fig. 4, dashed line). The best fit of the rainfall-dependent models was the discrete logistic with T = 4 years (Table 2). This model fit the census data better than the above simple logistic model, and accounted for the rise and then drop in the number of vicuñas (Fig. 4, solid line). The fit of the rainfall-dependent models varied quite a bit depending on T, the size of the rainfall time lag allowed, with the best fit for T = 4 years and a poorer fit for both smaller and larger values of T (Table 2; Appendix I).

Vicuña density varied highly across the census region from 50 to 1,350 vicuñas on average per sector, and 0–13 vicuñas/km². The number of vicuñas in a given sector was not clearly related to the amount of bofedal area in that sector, although there did seem to be a quadratic relationship with the highest number of vicuñas in sectors with intermediate bofedal area (Fig. 5A). The number of domestic animals, on the other hand, was significantly positively correlated with bofedal area in each sector (Fig. 5B; $r^2 = 0.67$, $P < 0.01$).

The spatial distribution of vicuñas across sectors also changed over the past 30 years. The fraction of the total number of vicuñas found in the highest quality sectors (defined as those sectors that were made up of at least 4% bofedales; sector numbers 4, 6, 7, 11, 12, 16, and 24) changes over time; most notably it significantly increases after the
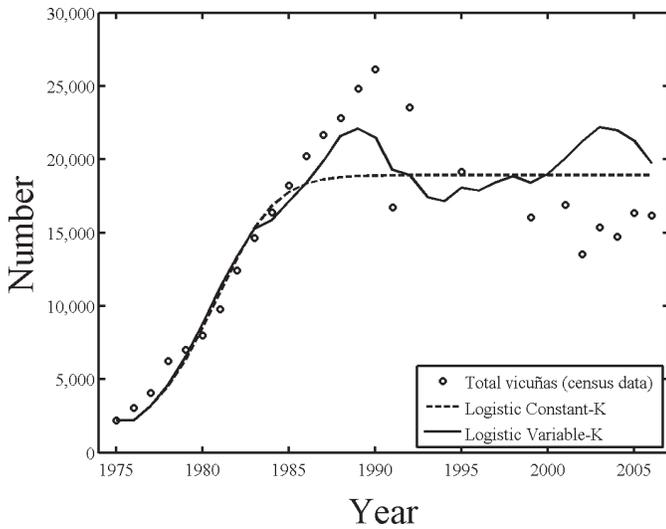
Fig. 4.—Total number of animals from the vicuña census data (circles), the best fit of the simple logistic model (dashed line), and the best fit of the rainfall-dependent models: the logistic model with T = 4 (solid line).

population drop starting in 1991 (significant difference between 1975–1990 and 1991–2007; $P < 0.01$, Mann–Whitney U-test).

Discussion

We have shown that a model with a fluctuating carrying capacity fits the vicuña census data better than a simple logistic model. Past analyses of this same data set have suggested that vicuñas were following exponential (Cattan and Glade 1989) or simple logistic (Bonacic et al. 2002) growth. Although these studies have suggested that vicuña dynamics likely depend on rainfall and primary productivity, ours includes these effects directly by allowing the carrying capacity to fluctuate as a function of rainfall, thereby accounting for the links between rainfall, primary productivity, and vicuña carrying capacity.

Allowing the carrying capacity to depend on rainfall in a model of herbivores in semiarid systems is a logical extension of a constant carrying capacity model; studies on several continents have shown that rainfall not only affects primary productivity (Africa—Breman 1975; North America—Lauenroth and Sala 1992; and South America—Yahdjian and Sala 2006), but that its effects can extend to the herbivore level (Australia [Caughley and Gunn 1993], Africa [Mills et al. 1995], and South America [Oesterheld et al. 1992]). Indeed, allowing carrying capacity to depend on rainfall in ungulate population dynamics models is almost the norm for African systems such as elephants, wildebeest, and zebras (e.g., Breman 1975; Chamaille-Jammes et al. 2008; Georgiadis et al. 2003; Pascual et al. 1997), but has rarely been used in models of ungulate populations from other continents.

Rainfall often has lag effects: primary productivity alone has been shown to be affected by the last 1–2 years of rainfall in semiarid systems in both North and South America
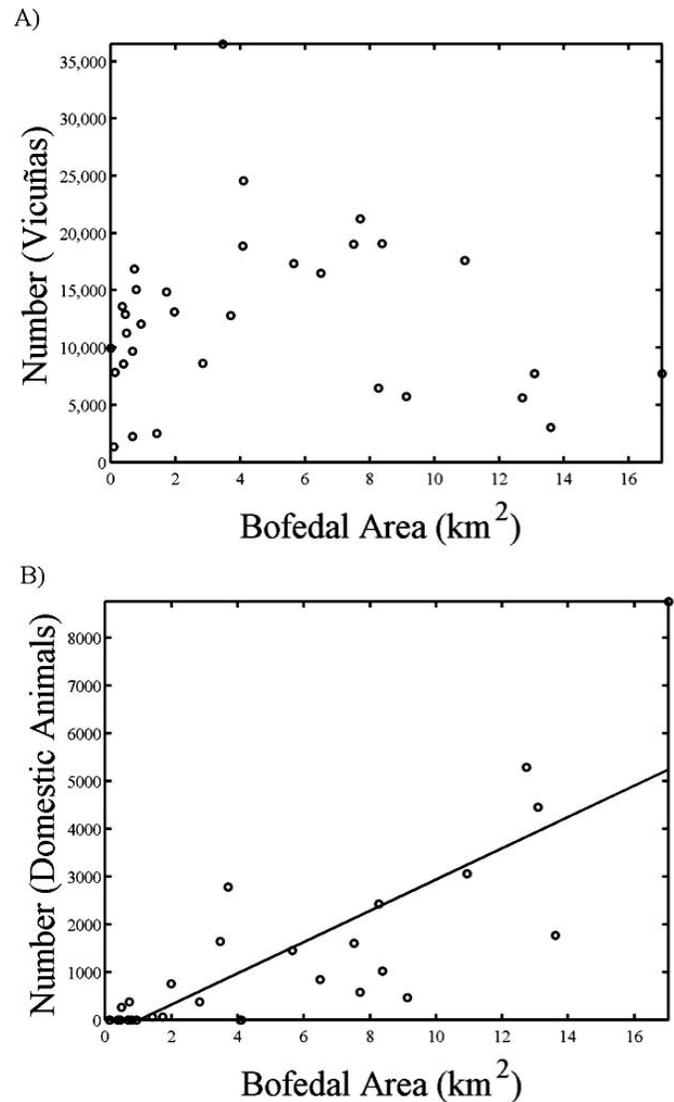

Fig. 5.—Relationship between the average number of animals per sector (averaged across data from 2000, 2001, and 2003–2006), and bofedal area (in km^2) per sector. A) Number of vicuñas (no clear relationship), and B) number of domestic animals (correlation $r^2 = 0.6674$, $P < 0.00001$).

(Oesterheld et al. 2001; Yahdjian and Sala 2006), and herbivore dynamics have been found to correlate with rainfall with lags of years to decades (Caughley and Gunn 1993; Mansson et al. 2007; Ogutu and Owen-Smith 2005; Ogutu et al. 2008). To account for this, in our models we allowed carrying capacity to depend on the average rainfall from the previous several years, with the best-fit model depending on rainfall during the past 4 years (T = 4). Vicuñas start reproducing around age 3 (Galaz 2005), suggesting that the mechanism for the time lag in our model may be related to the existence of a link between fecundity of adult vicuñas and the amount of nutrients and water they had access to during their first 3–4 years of life. Further studies, however, are required to test for this potential mechanism.

We have shown that our rainfall-dependent models, which allow carrying capacity to vary in time as a function of

rainfall, are able to capture the drop in vicuña numbers during the early 1990s. In contrast, the constant carrying capacity models do not capture this drop or the following fluctuations, and instead level off once the vicuña population reaches its carrying capacity. However, even our rainfall-dependent models did not fully explain the steep drop in population size from 1990 to 1991. This may be due in part to an error in the census data set. In the years 1989, 1990, and 1991, the census count was lower than expected based on the previous years of census data. This was assumed to have been the result of a methodological error during the census and the data were corrected to be higher than the number of vicuñas actually counted. Here, we have reported the original census data for 1991; however, the original data for 1989 and 1990 are not available so we have included the corrected counts for these years.

Additionally, although our model predicts large fluctuations in population size during the late 1990s and early 2000s, the actual population size has relatively small fluctuations during this time. There are 2 potential explanations for this. First, it is possible that high vicuña densities during the late 1980s led to overgrazing and caused long-lasting damage to the ecosystem (Rabinovics et al. 1991), which would lead to a longer delay in the recovery of primary productivity, and in turn of vicuña numbers, than otherwise predicted. Second, a changing spatial configuration of vicuñas could result in altered population dynamics. Our model is not spatially explicit, and therefore assumes that the spatial distribution of vicuñas is constant over time, and more specifically, that fluctuations in rainfall have the same effect on vicuña numbers across space. Because bofedales have water year-round, they are likely to be more robust to fluctuations in rainfall than other areas of the puna that are dependent on rainfall as their only source of water. Therefore, vicuñas in sectors with different amounts of bofedal area are likely to be affected quite differently by variation in rainfall. We show, in our analysis of the spatial patterns in vicuña data, that the spatial distribution of vicuñas changes significantly during the early 1990s. Furthermore, we found that their distribution shifts with respect to bofedal area, with vicuñas in sectors with more bofedales after the drop. Therefore, because the influence of rainfall changes over space (depending on how many bofedales are in a sector) and vicuña spatial distribution changes over time, the influence of rainfall on vicuña numbers changes over time as well. This goes against our implicit assumption of constancy in space, and likely explains the discrepancy between the census data and our model. It is likely that regions with many bofedales act to buffer the effect of rainfall fluctuations on vicuñas (''buffer effect''— Kluyver and Tinbergen 1953), which potentially explains why the number of vicuñas is fairly constant (buffered) from the mid-1990s onward, instead of fluctuating as greatly as the model predicted. This concept, that the spatial distribution of individuals could act to mediate density-dependence, also has been suggested for vicuñas based on observations of individual habitat choice (Arzamendia et al. 2006).

Even though vicuñas spend much of their time foraging in bofedales (Renaudeau d'Arc et al. 2000), the number of vicuñas in a sector was not clearly related to bofedal area by sector (Fig. 5A). There are several possible explanations for this. First, as mentioned, because the distribution of vicuñas across sectors changed over the course of 30 years, this could have blurred the relationship between vicuñas and bofedal area. However, this is unlikely to be the case because the distribution of vicuñas across sectors, just using census data from 1991 to 2006, is still not significantly related to bofedal area (results not shown); the same is true for just using census data from 1975 to 1990. A 2nd possibility is that because bofedales make up such a small fraction of a census sector, that bofedal area in a sector is not a good predictor of the total number of vicuñas in the entire sector. One way to test this would be to record the habitat location of vicuñas during the census, with the prediction that vicuñas would be found most commonly in bofedales. However, if this is done, the time of day also should be recorded because vicuñas are known to vary their habitat use over the course of the day (Vilá and Cassini 1993). A 3rd explanation is that the presence of domestic animals in the bofedal areas limits the availability of these areas for vicuñas (Villalba 2003). This is likely to be a possibility because the number of domestic animals was significantly related to bofedal area by sector. This means that those sectors that are the most desirable in terms of bofedal area also would have the highest amount of competition with domestic animals (Fig. 5B).

We have shown that the vicuña population in Chile appears to be growing, according to a logistic growth model where the carrying capacity is modified by rainfall, which acts through primary productivity. Our study highlights the importance of establishing long-term monitoring efforts, including periodic reanalysis of the entire data set over time, in order to gain novel insights into the system being studied (see also Lindenmayer et al. 2010). It is vital, therefore, that vicuñas in Chile continue to be monitored and censused, so that we can continue to gain an understanding of the factors influencing vicuña population dynamics. Further insight into the spatial patterns and habitat use of vicuñas could be gained if the type of habitat vicuñas were found in was noted during the census. Additionally, following several individuals across many years could help elucidate mechanisms leading to such a long lag between rainfall and population numbers. Finally, our study contributes to the general understanding of ungulate population dynamics on a global scale, by bringing a novel South American species to a discussion that has primarily been dominated by African species.

RESUMEN

La vicuña (*Vicugna vicugna*) es un camélido sudamericano que llegó a estar en riesgo de extinción debido a la presión de caza en el altiplano de los Andes centrales. Luego del inicio de los esfuerzos por conservar la especie, sus poblaciones se recuperaron hasta quedar fuera de peligro en la clasificación de Unión Internacional para la Conservación de la Naturaleza y los Recursos Naturales. En la presente publicación se

presenta un análisis de 31 años de datos de censo de vicuñas en una zona del norte de Chile para investigar la influencia de varios factores sobre la dinámica poblacional de ésta especie. La dinámica poblacional durante los primeros 15 años esta dominada por el fuerte crecimiento de la población como consecuencia de su recuperación de la caza excesiva. En los siguientes 15 años las dinámicas son dominadas por las fluctuaciones en torno a la capacidad de carga de la zona. En este trabajo encontramos que el major modelo que explica la dinámica observada es un modelo logístico que toma en cuenta cómo los cambios en la precipitación y la productividad primaria conducen a fluctuaciones en la capacidad de carga, lo que sugiere que los recursos que limitan el tamaño de la población de vicuñas no son constantes, sino que cambian con el tiempo. También se observa que la distribución espacial de las vicuñas cambia a través del tiempo en relación a la oferta de alimentación existente en los bofedales, que corresponde a la oferta más nutritiva de la zona. Finalmente, este trabajo demuestra la importancia de contar con bases de datos de largo plazo para entender los factores que afectan la dinámica de estas poblaciones y sugiere que una mayor comprensión se podría lograr si se registrara la ubicación de los individuos, en relación al tipo de hábitat, durante el censo.

ACKNOWLEDGMENTS

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APPENDIX I

Estimates of the parameters T (in years), K_0 (in individuals), α, and r; the number of variables (k); Akaike information criterion, corrected for small sample size (AIC_c) scores; differences in AIC_c scores between each model and the top-ranked model (ΔAIC_c); and r^2 values. Shown are the results for all 3 models and all time lags.

Model	T	K_0	α	r	k	AIC_c	ΔAIC_c	r^2
Constant carrying capacity models								
Logistic	—	18,930	—	0.5157	2	406.26	8.07	0.75
Ricker	—	18,940	—	0.4495	2	406.72	8.53	0.75
Beverton–Holt	—	29,390	—	1.645	2	407.36	9.17	0.74
Rainfall-dependent carrying capacity models								
Logistic	1	11,580	26.55	0.4944	4	406.55	8.36	0.80
Logistic	2	8,000	37.48	0.5013	4	403.82	5.64	0.82
Logistic	3	8,000	36.84	0.5095	4	401.66	3.48	0.83
Logistic	4	8,000	36.76	0.5189	4	398.19	0.00	0.85
Logistic	5	8,000	36.52	0.5191	4	399.38	1.19	0.85
Logistic	6	8,000	36.36	0.5151	4	400.96	2.78	0.84
Logistic	7	8,000	36.20	0.5094	4	403.07	4.89	0.82
Logistic	8	8,000	35.98	0.5063	4	404.38	6.20	0.81
Logistic	9	8,000	35.62	0.5008	4	406.65	8.47	0.80
Logistic	10	8,000	35.32	0.4962	4	408.12	9.93	0.78
Logistic	11	8,000	35.02	0.4947	4	408.45	10.27	0.78
Logistic	12	8,000	34.74	0.4942	4	408.49	10.30	0.78
Logistic	13	8,059	34.36	0.4963	4	407.67	9.48	0.79
Logistic	14	8,038	34.27	0.4986	4	406.85	8.66	0.79
Logistic	15	8,000	34.32	0.5017	4	405.76	7.57	0.80
Ricker	1	10,080	31.82	0.4344	4	405.87	7.68	0.80
Ricker	2	8,000	37.30	0.4431	4	403.39	5.21	0.82
Ricker	3	8,000	36.81	0.4478	4	401.60	3.41	0.83
Ricker	4	8,000	36.75	0.4515	4	399.26	1.07	0.85
Ricker	5	8,000	36.53	0.4497	4	400.85	2.67	0.84
Ricker	6	8,000	36.35	0.4458	4	402.60	4.42	0.83
Ricker	7	8,000	36.16	0.4412	4	404.66	6.47	0.81
Ricker	8	8,000	35.92	0.4384	4	405.93	7.74	0.80
Ricker	9	8,000	35.57	0.4347	4	407.83	9.65	0.79
Ricker	10	8,000	35.27	0.432	4	408.96	10.77	0.78
Ricker	11	8,059	34.80	0.4315	4	409.12	10.93	0.77
Ricker	12	8,071	34.50	0.4319	4	408.98	10.80	0.78
Ricker	13	8,052	34.37	0.4337	4	408.13	9.95	0.78
Ricker	14	8,000	34.40	0.4356	4	407.31	9.12	0.79
Ricker	15	8,000	34.32	0.4382	4	406.35	8.16	0.80
Beverton–Holt	1	13,550	60.77	1.62	4	405.33	7.14	0.81
Beverton–Holt	2	8,000	75.96	1.627	4	402.35	4.17	0.83
Beverton–Holt	3	8,000	74.49	1.629	4	400.38	2.20	0.84
Beverton–Holt	4	8,043	74.44	1.628	4	398.29	0.10	0.85
Beverton–Holt	5	8,000	75.00	1.622	4	400.46	2.27	0.84
Beverton–Holt	6	8,000	75.96	1.613	4	402.61	4.42	0.83
Beverton–Holt	7	8,000	76.93	1.605	4	404.89	6.71	0.81
Beverton–Holt	8	8,000	77.36	1.599	4	406.27	8.08	0.80
Beverton–Holt	9	8,000	77.54	1.594	4	408.18	9.99	0.78
Beverton–Holt	10	8,000	77.56	1.59	4	409.19	11.00	0.77
Beverton–Holt	11	8,000	76.98	1.59	4	409.12	10.93	0.77
Beverton–Holt	12	8,071	75.90	1.592	4	408.77	10.58	0.78
Beverton–Holt	13	8,000	75.11	1.596	4	407.66	9.47	0.79
Beverton–Holt	14	8,000	74.10	1.6	4	406.67	8.49	0.80
Beverton–Holt	15	8,000	73.07	1.605	4	405.59	7.40	0.80