Density dependence in the camelid *Vicugna vicugna*: the recovery of a protected population in Chile

C. Bonacic, D. W. Macdonald, J. Galaz and R. M. Sibly

Abstract The vicuña *Vicugna vicugna* is a wild South American camelid. Following over-exploitation, which brought the species to the brink of extinction in Chile in the 1960s, the population was protected. Since 1975 the population has been censused annually, generating one of the most extensive long-term census databases for any South American mammal. In this paper we use these data, and measures of environmental parameters, to describe the population growth trend of the species and to estimate carrying capacity. Our results indicate that the vicuña has been protected successfully in northern Chile. The census data reveal that, following protection, the population displayed logistic growth between 1975 and 1992. Population growth rate declined linearly with population size, which indicates a degree of density dependence. Density independent factors, such as rainfall, may also have been important. The principal density dependent effect observed was that birth rate declined in those family groups with the most breeding females. The

carrying capacity of the study area was estimated from the census data and from models based on precipitation and local primary productivity. Using the census data, an estimation of carrying capacity as the asymptote of the fitted logistic curve suggested that the vicuña population should reach approximately 26,000 vicuñas, whereas estimation when the population growth rate was equated to zero gave a carrying capacity of *c.* 22,000. Coe's method based on local precipitation predicted 31,000 vicuña, whereas Lavenroth's method based on local primary productivity predicted 26,000 vicuña. In reality, the census data showed that the population peaked at 22,463 vicuñas in 1990. The results are discussed in relation to the need for better census techniques and the implications of density dependent effects for the management of the vicuña in Chile.

Keywords Carrying capacity, Chile, density dependence, population growth rate, vicuña, *Vicugna vicugna*.

Introduction

Vicuña *Vicugna vicugna* (Camelidae) inhabit the Andean *puna* ecosystem (grassland of low productivity situated on a high plateau) at altitudes of 3,000–4,600 m (Torres, 1992).Their range currently extends from latitudes 9°30′ S to 29°00′ S. In the 16th century vicuñas numbered several million (Koford, 1957; Torres, 1992). However, excessive commercial hunting with guns and dogs for the vicuña's valuable wool during the 20th century caused the population to decline to 400,000 by the early 1950s (Koford, 1957; Franklin, 1982). In the late 1960s there were fewer

than 2,000 vicuña in Bolivia, Chile and Argentina combined, and 5,000–10,000 in Perú (Rabinovics *et al.*, 1991). Perú and Bolivia signed an agreement for the conservation of the species in 1969, and active conservation commenced at Pampa Galeras Natural Reserve in Perú in 1965. Shortly afterwards, in the early 1970s, Chile and Argentina signed the Vicuña Convention (Eltringham & Jordan, 1981). The vicuña is currently categorized as Lower Risk: conservation dependent on the 2000 IUCN Red List (Hilton-Taylor, 2000), and it and its products are listed in CITES Appendix I (Torres, 1992), which prohibits all trade, and was ratified by all the states concerned in 1973 (Wheeler & Hoces, 1997). In the late 1970s, the five states comprising the range of the vicuña signed the Agreement for the Conservation and Management of the Vicuña (ACMV), embracing protection, conservation, and sustainable utilisation (CITES, 1997). In Chile a long-term conservation programme was initiated in 1970 by the Chilean Forestry Service (CONAF), when the national population was estimated at *c.* 600 animals (Cattan & Glade, 1989). This conservation programme involved the creation of protected areas in the northern Chilean altiplano or *puna* in Parinacota Province, where vicuña have subsequently been counted annually (Galaz, 1998).

C. Bonacic[1] (Corresponding author) and **D.W. Macdonald** Wildlife Conservation Research Unit, University of Oxford, Department of Zoology, South Parks Road, Oxford OX1 3PS.

J. Galaz Corporación Nacional Forestal, Casilla 1484 Arica-Chile.

R.M. Sibly University of Reading, School of Animal and Microbial Sciences, Whiteknights, PO Box 228, Reading RG6 6AJ.

[1] Present address: Department of Animal Science, Faculty of Agriculture and Forestry Science, Pontificia Universidad Catolica de Chile, Casilla 306, Correo 22, Santiago-Chile. E-mail: bonacic@puc.cl

118

The 1997 CITES Convention authorised the sale of 3 tonnes of stockpiled vicuña wool and the development of a trade in raw fleeces from Perú (CITES, 1997). This decision opened the market for vicuña wool after more than 30 years of protection. The possibility of a sustainable harvest of vicuña wool is extremely important for the *Aymara* and *Quechua* Indian communities that inhabit the vicuña range (Torres, 1992). Sustainable use of the vicuña in Peru involves the capture and shearing of wild animals (Wheeler and Hoces, 1997), but the possible consequences of these practices for the survival of the vicuña are still unknown. Vicuña in Chile will soon be managed in a way that allows regular shearing, adding urgency to the need for population analysis to quantify potential production and any impacts on the population.

Previous descriptions of population growth of vicuña in Perú (Hoffmann *et al.*, 1983; Cueto *et al.*, 1985), Argentina (Rabinovich *et al.*, 1985; Rabinovics *et al.*, 1991) and Chile (Rodriguez & Nunez, 1987; Cattan & Glade, 1989) were restricted to time series of no greater than 10 years. Here we present a 17-year database of vicuña population counts in Chile, which is the most enduring population monitoring of a medium-sized mammal carried out in this country (Galaz, 1998). We have analysed trends in this population following its protection, both to understand the natural processes affecting the vicuña, and to establish a baseline from which to assess the impact of the commercial use of the species. In addition, long-term population monitoring of this ungulate in the extreme environmental conditions of the altiplano provides information that can be compared to previous studies conducted on ungulates of similar size from other environments (Caughley, 1980; Clutton-Brock & Albon, 1982). The lack of replicates is a central problem in ecology, making it useful to verify in South American wild camelids the patterns of population growth established for other species. The resulting knowledge is a prerequisite for sound management; hitherto little was known about the factors regulating vicuña populations (Eltringham & Jordan, 1981).

The aims of this study were: (1) to describe the population dynamics of the vicuña since the programme of protection and annual monitoring began, and (2) to estimate carrying capacity for the species using models based on rainfall and primary productivity to test whether density dependent effects were acting on this population.

Methods

The study area comprised approximately 4,900 km² within the Province of Parinacota in the Tarapacá Region of Chile (19°00′ S 69°30′ W, Fig. 1), which historically contained most of the country's vicuña population (Torres, 1992; Galaz, 1998). The altiplano is a dry, cold, windy steppe with insufficient rainfall for most crops, and frequent frosts, even in summer. The mean annual temperature during the study period was 5.1°C at the Parinacota weather station at 4,390 m (69°09′ S, 18°12′ W) (INIA, 1989). July is the coldest month, with a mean temperature of −0.04°C, and January the warmest (mean 7.9°C). The mean annual precipitation is 321 mm. Groundwater from melting ice creates locally moist edaphic conditions where hardy grass grows abundantly in so-called *bofedales*. *Bofedales* are permanently wet areas located near streams, ponds or lakes, and have a continuous cover of herbs, rushes and grasses.

The census area spans, from north to south, the farmland of Caquena, Lauca National Park (a Biosphere Reserve) and Las Vicuña Natural Reserve (a national protected area). Census data for 1975–1992 were provided by the Chilean Forestry and Wildlife Service (CONAF) (Fig. 2) (Galaz, 1998). Data from after 1992 were discarded because the census methodology was changed. CONAF staff surveyed the whole study area annually using a standard protocol (Rodriquez & Nunez, 1987; Cattan & Glade, 1989). The survey teams partitioned the area into sectors bounded by identifiable ground features such as streams, slopes and cliffs, and within each site they followed 2–3 fixed routes, each separated by *c*. 3 km, (Torres, 1992; Galaz, 1998). Using binoculars all observable vicuña were counted in the census area. It is assumed that population size was constant during each 2–3 week census period. The censuses were timed to take place after the annual expulsion of male yearlings from the family groups, which occurs in November (Franklin, 1976; Vila & Cassini, 1993). Male yearlings were therefore counted as members of bachelor groups. Vicuña, like other South American camelids, are not sexually dimorphic and because they cannot be aged without dental examination, individuals were classified based on behaviour and group structure (Hoffmann *et al.*, 1983; Cueto *et al.*, 1985; Torres, 1987). Vicuña were categorized into family groups (one leader male, several females and calves), male groups (bachelor males with no clear leader), and solitary animals (adult males displaced from family groups) (Hoffmann *et al.*, 1983). The term leader male refers to the dominant male that defends a territory and breeds with females within its group (Hoffmann *et al.*, 1983). Gestation lasts 11.5 months and the calving season is January–March each year (Cattan & Glade, 1989). Calves can be recognized in the field from their smaller size compared with bachelors and adults, their woolly appearance, and differing behaviour (Vila & Cassini, 1993). At the time of the census, calves were still clearly distinguishable from bachelors and adults.
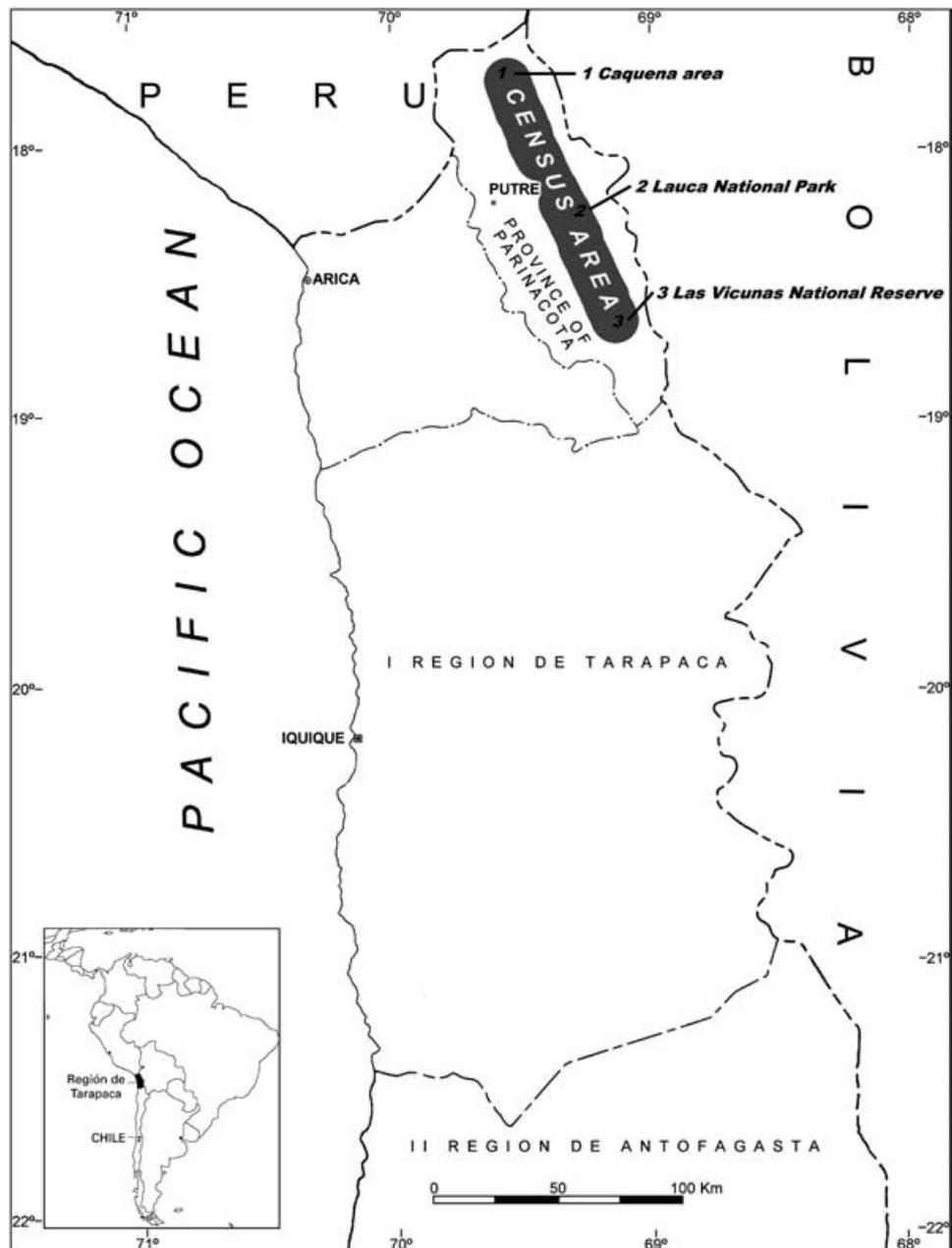
Fig. 1 Location of the census area (shaded) for vicuña *Vicugna vicugna* on the altiplano in the Province of Parinacota in the north of the Tarapacá Region of Chile. The inset indicates the position of the Tarapacá Region in South America.

To determine census error Rodriguez & Nunez (1987) analysed a shorter data series by undertaking a second count at a randomly chosen sub-sample of sites. This error estimation was undertaken for two different years (n = 5 sites in 1980 and n = 15 sites in 1982) and the repeated counts duplicated precisely the routes and protocols described above. Rodriguez and Nuñez (1987) obtained a census error estimate of 0.4% for the sites sampled in 1980. A mean standard error of 77 animals

(1.45%) was calculated with no significant differences between counting for a second estimation error in 15 sites during 1982 (ANOVA $F_{1,14} = 8.84$, $P > 0.05$), providing an estimated census error of 1.45%.

Population data analysis
The logistic equation was fitted to the relationship between the size of the population and its growth rate. The S-curve model fits the Pearl-Reed logistic trend
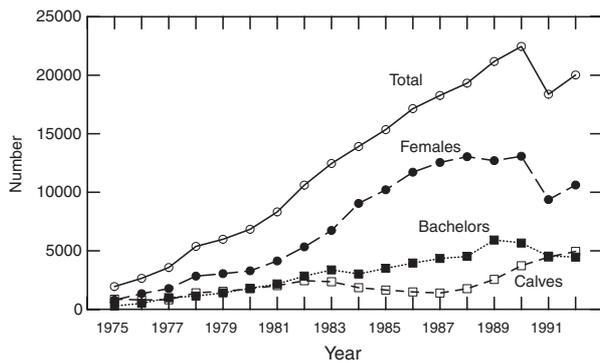
Fig. 2 Number of vicuña present in the study area during 1975–1992. Total numbers are shown, together with numbers of females, bachelor males and calves.

model (Minitab, 1996), in which the series follows an S-shaped curve. Following Begon *et al.* (1996), the annual increase or decrease (from year t to t + 1) in the population, λ, was calculated as $r = \log_e \lambda$, where r is the intrinsic rate of change.

The logistic model assumes that the early growth of a population $N(t)$ increases exponentially with a growth rate constant a. As the population $N(t)$ approaches a limit, k, the growth rate $(dN(t))/dt$ slows, producing the characteristic S-shaped curve of the relationship between population size and time (Caughley, 1980). The mechanisms that cause this slowing-down depend on characteristics of the population or system being modelled, but empirical studies have shown that this effect occurs in many species (Caughley, 1980). Thus, the logistic model $(10^a/[\beta_0 + \beta_1*(\beta_2)^t]$, where a, β_0, β_1 are values obtained from the algorithm that fits the trend) is a useful generic model both for systems where the mechanisms are understood and those in which the mechanisms remain obscure (Caughley, 1981).

The vicuña's territoriality and social organisation facilitate the precision of total counts (Hoffmann *et al.*, 1983; Svendsen & Bosch, 1993). However, a caveat is that larger groups might have contained non-reproductive females; this potential bias can be dismissed on the grounds that our field data from 400 captured animals revealed few females in bachelor groups (Bonacic, 2000).

Carrying capacity
Population and environmental parameters were used to achieve estimates of carrying capacity (K). We used the logistic curve of population growth to estimate K in two ways: 1) by fitting a logistic curve to the time series, and 2) by plotting population growth rate against population size. In the former, carrying capacity is estimated when an asymptotic trend is achieved. In the latter, carrying capacity is estimated when $r = 0$.

We compared these two estimations of K with estimates of K from two models based on environmental factors. For these models we assumed that total herbivore density has a limit imposed by the carrying capacity of the study area, so K for vicuña will be devalued by the presence of domestic livestock. The K available for vicuña can be assessed if the total stocking rate of livestock expressed in vicuña units is known (Rabinovics *et al.*, 1991): Carrying capacity available for vicuña (K_a) = total K – livestock load. According to annual records of the Animal Health Office, populations of domestic stock in the study area were approximately 31,000 alpaca, 41,000 llama and 31,000 sheep (Galaz, 1998). It has been suggested that the estimated equivalence factor for the stocking rate of these three species compared to vicuña is 1 : 1.4 : 1.63 : 1.4 vicuña : alpaca : llama : sheep. On this basis the estimated aggregated number of domestic ungulates was equivalent to 155,000 vicuña (Rabinovics *et al.*, 1991). These equivalencies were based on body weight, and ignore subtleties of food selectivity and habitat preferences.

Total carrying capacity was then estimated in two ways: using Coe's method based on local precipitation and Lavenroth's method based on local primary productivity. Coe *et al.* (1976) estimated the carrying capacity of African savannah using the precipitation-biomass regression method ($y = -1.2202 + 1.7596x$ where $y = \log_{10}$ herbivore biomass (kg km^{-2}) and $x = \log_{10}$ rainfall (mm yr^{-1})). Rabinovics *et al.* (1991) used this method to estimate primary productivity and carrying capacity of the Argentine *puna*. We extended this analysis, with additional data from the Chilean and Peruvian *puna*. The division of total herbivore biomass by adult body weight (40 kg for an adult vicuña) provides an estimate of carrying capacity (Rabinovics *et al.*, 1991).
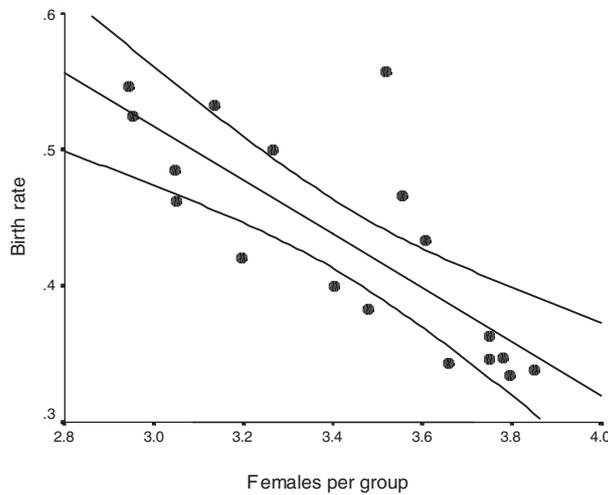
Lavenroth's estimator of Net Aerial Primary Productivity (NAPP) incorporates 55 grassland measurements from around the world. Rabinovics *et al.* (1991) adjusted this estimator to the altiplano conditions of South America, adding five additional points from Argentinean and Peruvian dry grassland, to produce an estimate of primary productivity (kg dry matter ha^{-1} yr^{-1}). Taking 1 kg of dry matter per individual as the daily requirement of the adult vicuña and 10% intake efficiency allows the total carrying capacity to be estimated in 'vicuña units'.
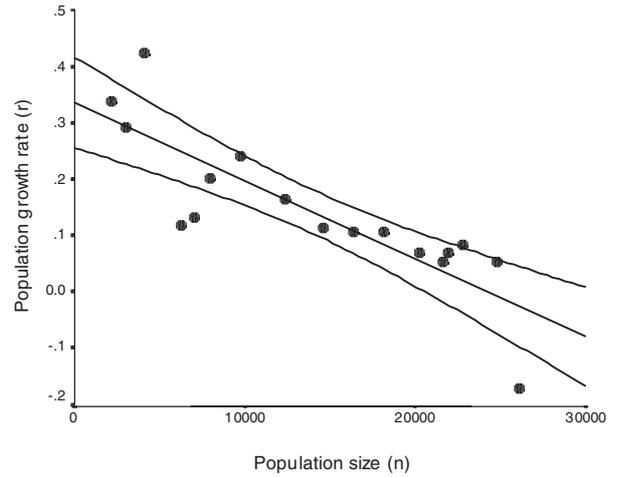
Results

Between 1975 and 1992 the vicuña population increased tenfold from *c.* 2,000 to >20,000, following 17 years of protection (Fig. 2). Vicuña density increased from 0.4 km^{-2} in 1975 to a peak of 4.5 km^{-2} in 1990. The mean family group size was 4.9 ± 0.3 (SD) vicuña. The higher the

proportions of females in a family group the lower the number of calves per female (Fig. 3). In 1990, 34% of females had calves that survived to become yearlings and this fell to 25% one year later (the delayed effect of 11 months of gestation).

The population increase fitted the logistic curve: $N(t) = 10^5/(3.79 + 53.39(0.732)^t)$ where $N(t)$ is population size for each year after 1975. The asymptote of the curve is $26,398 \pm 673$ animals, which provides an estimate of the carrying capacity of the census area. Similar calculations yield estimates for each age and sex class (Table 1). Population growth rate declined linearly with population size (Fig. 4), according to the logistic equation. From this, population size when population growth rate r is zero is estimated as $22,349 \pm 1,627$ vicuña, and this provides a second estimate of the carrying capacity of the census area.

Fig. 4 Population growth rate (r) plotted against total population size. The significant relation between population growth rate and population size suggests density dependence (R^2 adjusted $= 0.68 \pm 0.007$ (SE); $F_{1,16} = 35.5$, $P < 0.001$).

Fig. 3 Birth rate and family group size, expressed as number of adult females per group (R^2 adjusted $= 0.59 \pm 0.005$ (SE); $F_{1,16} = 25.5$, $P < 0.001$). Birth rate is estimated as mean number of calves per female. It is possible that calves are underestimated because of the date of the census (see Discussion).

Based on precipitation the estimated total carrying capacity of the study area was 185,949 vicuña. The carrying capacity estimated from primary productivity was 36.9 vicuña per km², which yields a total potential carrying capacity for the whole area of *c.* 181,000 'vicuña units'. Given that the domestic livestock in the area (stocking rate has been approximately constant during the last ten years; Galaz, 1998) are equivalent to 155,000 vicuña, the estimated carrying capacity for vicuña is *c.* 31,000 based on precipitation and *c.* 26,000 based on primary productivity.

The mean estimate of carrying capacity, using the two estimates based on the logistic model and those based on precipitation and net primary productivity, is $26,424 \pm 2,736$ (SE) vicuña for a census area of 4,900 km².

Table 1 Fitted logistic growth model (see text for details) for the time series of the vicuña population between 1975 and 1992.

Time series	Equation	Intercept	Asymptote	MAPE (%)	MAD
Population	$Yt = 10^5/(3.78814 + 53.3885*(0.731892^t))$	1,749	26,398	5	673
Females	$Yt = 10^5/(7.61808 + 142.953*(0.714926^t))$	664	13,126	13	979
Yearlings	$Yt = 10^5/(19.1346 + 370.383*(0.693907^t))$	256	5,256	12	323
Bachelors	$Yt = 10^5/(33.4275 + 109.695*(0.827565^t))$	698	2,991	27	613

Equation terms based on the curve fitting analysis of Minitab (Minitab, 1996):
Intercept: Estimated number of animals at time $t = 0$.
Asymptote: Estimated carrying capacity when calculated trend reaches the asymptote.
MAPE: Mean absolute % error: measures the accuracy of fitted time series values.
MAD: Mean absolute deviation; measures the accuracy in number of animals.

Discussion

The analysis of patterns of population growth of the Chilean vicuña population over 17 years suggests that density dependent factors at least partially explain the trend in population growth rate; however, the scatter in the relationship may indicate that density independent factors are also involved. As family group size increased, the number of offspring per female decreased, suggesting one mechanism whereby density dependence may operate (Fig. 3). In other species, correlations of this sort have been used to infer density dependence (Clutton-Brock & Albon, 1982; Begon et al., 1996; Sibly et al., 2000). A different, but not necessarily exclusive, explanation is that social behaviour constrains group size and that optimum group size is unaffected by population density (Vila & Roig, 1992). In this case, however, we believe that the extent of the reduction in birth rate suggests an underlying density dependent effect, irrespective of any moderating influence of social organisation.

Cattan & Glade (1989) described an initial linear trend in growth between 1975 and 1985 for the same population. They predicted the logistic trend we have revealed. Indeed, only one year later, in 1986, the decelerating process started with a decline in population growth rate from $r = 0.1$ in 1985 to $r = 0.06$ in 1986. It seems likely that this decline was a result of overgrazing (Caughley, 1981).

Similar fluctuations have been recorded for vicuña in Pampa Galeras (Perú) between 1976 and 1979 (Brack, 1980, cited by Eltringham & Jordan, 1981). Brack (1980) estimated a growth rate of 3% in 1976 and 30% in 1977, but during the following year the population declined by 13%. However, these figures have been questioned (Eltringham & Jordan, 1981). In our study area in 1992, as in Pampa Galeras in 1980, population declines coincided with a reduction in the number of calves. In Pampa Galeras 85% of adult females produced calves in 1974, of which 76% survived until the end of the year in their first season (Franklin, 1976). However, in 1980, after steady population growth, the pregnancy rate in Pampa Galeras was estimated at 58%. Twenty-four percent of females produced a calf, of which only 27% were still alive in October (Hoffmann et al., 1983). In our study, and before the population started to decline, larger numbers of females per male in each family group correlated with fewer calves per adult female. The decline began in 1990, when the calving rate was low and adult females appeared to be in poor condition. In contrast, in 1991, when population decline had already lowered density, yearlings accompanied 52% of females. We suggest that long-term density-dependent relationships are modulated by between-year changes in precipitation and food availability, and that these factors explain the recovery of calf production in 1991, against the longer-term trend towards lower productivity. Our data do not allow a decisive test of the prediction that overgrazing and increased density are the cause of depressed reproductive success. That will necessitate simultaneous measures of the vicuñas' nutritional condition and grassland productivity; in future these data should be gathered in parallel with the continued annual census.

Analysis of our 17-year data series suggests that, in Chile, the population's growth slowed before it approached the estimated carrying capacity of c. 26,000 animals, and the population never reached the estimated asymptote of 26,398 animals (Table 1). Indeed, the population declined in 1990/1991 after reaching a density of 4.38 vicuña per km² (equivalent to 22,463 vicuña). Estimates of carrying capacity (in terms of herbivore biomass) based on rainfall and primary productivity agreed closely with estimates based on our population analysis. Using the correlation between grassland productivity and precipitation, Rabinovics et al. (1991) estimated a carrying capacity of 7.6–7.9 vicuña per km² for the Laguna Blanca reserve in Argentina, where mean annual precipitation was 130 mm. Hoffmann et al. (1983) described a population decline from a density of 7.5 vicuña per km² in Pampa Galeras, even though the mean annual precipitation was 463 mm. That the Chilean population reached carrying capacity at a lower density than reported by Rabinovics et al. (1991), despite the fact that the Chilean altiplano has a higher mean precipitation (321 mm) than Argentina, may be attributable to the greater degree of habitat degradation in the Chilean altiplano. This degradation is a result of overgrazing, mining and water extraction for large cities on the coast, the latter leading to the drying out of the meadows (Galaz, 1998).

Caughley (1981) pointed out that the most immediate effect of changes in population size is change in biomass availability, followed by long-term changes in plant composition. Despite their adaptations to local grasslands (for example, soft hooves) if vicuña exceed their carrying capacity on the altiplano they too are likely to cause botanical changes (Rabinovics et al., 1991). The recovery of the vicuña population and its growing need for grasslands have generated increasing competition with llama and alpaca ranching, which constitutes the basis of the economy of the local Aymara communities in the region (Torres, 1992).

The value of long-term census data is clear. In this case, continuing to monitor vicuña populations is a priority, as is the continual refinement of methodologies. The incorporation of distance sampling transect methods (Thomas et al., 1998) may improve the accuracy of the

population estimates, as may an evaluation of whether censuing in November risks an underestimate of calves. We conclude that protection probably saved this population from extinction, and that following a rapid recovery it began to fluctuate around current carrying capacity in 1992. Data from after 1992 were not included in the analysis because of a change in census methodology, but the general pattern from 1992–1996 was a fluctuating decline in population size. It is thus now necessary to perfect appropriate management to secure the future of both the vicuña and the *puna* ecosystem. A useful step would be to expand the monitoring system, and associated studies, to compare vicuñas living alongside domestic livestock with those isolated from such potential competitors, and to refine analyses to derive carrying capacities for different habitat types. This ecological knowledge must then be incorporated into a wider management plan for the species and region that considers the sustainable use of vicuña wool and the biological, ethical and economic considerations in its harvest.

Acknowledgements

References

Begon, M., Mortimer, M. & Thompson, D. (1996) *Population Ecology: A Unified Study of Animals and Plants*, 3rd edition. Blackwell Science, Oxford.

Bonacic, C. (1996) *Sustainable use of the vicuña* (Vicugna vicugna) *in Chile*. MSc thesis, University of Reading, UK.

Bonacic, C. (2000) *Ecology and physiology of the stress response in vicuña* (Vicugna vicugna). DPhil thesis, University of Oxford, UK.

Cattan, P. & Glade, A. (1989) Management of the *Vicugna vicugna* in Chile: use of a matrix model to assess harvest rates. *Biological Conservation*, **49,** 131–140.

Caughley, G. (1980) *Analysis of Vertebrate Populations*. Wiley, London.

Caughley, G. (1981) Overpopulation. In *Problems in Management of Locally Available Wild Animals* (eds P. Jewell, S. Holt & D. Hart), pp. 7–19. Academic Press, London.

CITES (1997) *Convention on International Trade in Endangered Species of Wild Fauna and Flora*: Appendices I and II and Interpretation (Fauna and Flora), Vol. 1997. CITES.

Clutton-Brock, T.H. & Albon, S.D. (1982) Competition and population regulation in social mammals. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 557–575. Blackwell Scientific Publications, Reading, UK.

Coe, M.J., Cummings, D.H. & Phillipson, J. (1976) Biomass production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22,** 341–354.

Cueto, L., Ponce, C., Cardich, E. & Rios, M. (1985) *Management of Vicuña: Its Contribution to Rural Development in the High Andes of Peru*. Food and Agriculture Organization of the United Nations, Rome.

Eltringham, S.K. & Jordan, W.J. (1981) The vicuña in Pampa Galeras National Reserve-the conservation issue. In *Problems in Management of Locally Available Wild Animals* (eds P. Jewell, S. Holt & D. Hart), pp. 277–289. Academic Press, London.

Franklin, W. (1976) *Socioecology of the vicuña*. PhD thesis, Utah State University, Utah.

Franklin, W. (1982) Biology, ecology and relationships to man of the South American camelids. In *Mammalian Biology in South America*, Vol. 6. Special Publication Series (eds M.A. Marer & H.H. Genoways), pp. 457–489. University of Pittsburgh, Pittsburg.

Galaz, J. (1998) El manejo de la vicuña en Chile. In *La Conservacion de la Fauna Nativa Chilena: Logros y perspectivas* (ed. V. Valverde), pp. 178. Corporacion Nacional Forestal, Santiago, Chile.

Hilton-Taylor, C. (compiler) (2000) *2000 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland, and Cambridge, UK.

Hoffmann, R.K., Otte, K.C., Prado, C.F.P. & Rios, M.A. (1983) *El manejo de la vicuña silvestre*. GTZ, Eschborn.

INIA (1989) *Mapa Agroclimatico de Chile*. Ministerio de Agricultura, Santiago, Chile.

Koford, C. (1957) The vicuña and the puna. *Ecological Monographs*, **27,** 152–219.

Rabinovich, J.E., Hernandez, M.J. & Cajal, J.L. (1985) A simulation-model for the management of vicuña populations. *Ecological Modelling*, **30,** 275–295.

Minitab (1996) *Minitab 11.21*. Minitab Inc., Philadelphia, USA.

Rabinovics, J., Capurro, A. & Pessina, L. (1991) Vicuña use and the bioeconomics of an Andean peasant community in Catamarca, Argentina. In *Neotropical Wildlife Use and Conservation* (eds J. Robinson & K. Redford), pp. 337–358. The University of Chicago Press, Chicago.

Rodriguez, R. & Nunez, R. (1987) El censo de poblaciones de vicuña. In *Tecnicas para el manejo de la vicuña* (ed. H. Torres), pp. 33–56. IUCN-PNUD, Santiago, Chile.

Sibly, R.M., Williams, T.D. & Jones, M.B. (2000) How environmental stress affects density dependence and carrying capacity in a marine copepod. *Journal of Applied Ecology*, **37,** 388–397.

Svendsen, G.E. & Bosch, P.C. (1993) On the behavior of vicuñas (Vicugna-Vicugna Molina, 1782) – Differences due to sex, season and proximity to neighbors. *Zeitschrift Fur Saugetierkunde-International Journal of Mammalian Biology*, **58**, 337–343.

Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strindberg, S., Hedley, S.L., Burt, M.L., Marques, F.F.C., Pollard, J.H. & Fewster, R.M. (1998) *Distance 3.5*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available at http://www.ruwpa.st-and.ac.uk/distance/

Torres, H. (1987) *Tecnicas para el manejo de la vicuña*. UICN-PNUMA, Santiago, Chile.

Torres, H. (1992) *South American Wild Camelids: An Action Plan for their Conservation*. IUCN, Gland, Switzerland.

Vila, B.L. & Cassini, M.H. (1993) Summer and autumn activity patterns in the vicuña. *Studies on Neotropical Fauna and Environment*, **28**, 251–258.

Vila, B.L. & Roig, V.G. (1992) Diurnal movements, family groups and alertness of vicuña (*Vicugna vicugna*) during the late dry season in the Laguna-Blanca-Reserve (Catamarca, Argentina). *Small Ruminant Research*, **7**, 289–297.

Wheeler, J. & Hoces, D. (1997) Community participation, sustainable use, and vicuña conservation in Peru. *Mountain Research and Development*, **17**, 283–287.

Biographical sketches

Dr. Cristian Bonacic received his DPhil in wildlife conservation from the University of Oxford, UK, in 2000. He is currently developing methods for evaluating stress associated with handling and shearing of wild vicuñas. In March 2001 he founded Fauna Australis, a Chilean research group that aims to tackle practical conservation problems.

Professor David Macdonald is head of the Wildlife Conservation Research Unit, Department of Zoology, University of Oxford. His main research interests include aspects of fundamental biology relevant to solving problems of wildlife conservation and environmental management.

Professor Richard Sibly has been in the Division of Zoology at the University of Reading, UK, since 1980. Prior to this he worked in the Department of Zoology at Oxford, where he obtained his doctorate. He is involved in a number of studies of the determinants of population growth rate and its role in population regulation.

Dr. Jose Luis Galaz joined the Chilean Wildlife Park Management Office in 1994, and is currently involved in GIS and wildlife ecology and management in northern Chile. He coordinated the vicuña project in Chile between 1994–2000.