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Demographic effects of live shearing on a guanaco population

Andrés Rey [a,*], Andrés J. Novaro [a,b], Mercedes Sahores [c], M. Laura Guichón [d]

[a] INIBIOMA, CONICET, Epulafquen 30 c2, 8371 Junín de los Andes, Neuquén, Argentina
[b] Patagonian and Andean Steppe Program, Wildlife Conservation Society, Curruhué 395 c2, 8371 Junín de los Andes, Neuquén, Argentina
[c] Vicealmirante O'Connor 369 7E, 8400 Bariloche, Río Negro, Argentina
[d] Departamento de Ciencias Básicas, Universidad Nacional de Luján, Rutas 5 y 6, 6700 Luján, Buenos Aires, Argentina

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ABSTRACT

Live shearing of wild guanacos (*Lama guanicoe*) is promoted as an alternative to livestock production and a conservation tool in the Argentinean Patagonia. However, biological sustainability of guanaco shearing has not been evaluated. We studied movements, population trends, survival, and yearling recruitment of guanacos, comparing sections with and without roundups on a Patagonian sheep ranch. A total of 2900 guanaco captures occurred in 10 roundups from 2003 to 2007. We estimated guanaco density and yearling/adult ratios with line transect surveys. We evaluated if guanacos left the section with roundups through direct observation of tagged guanacos and radiotelemetry. We estimated survival rate of shorn guanacos using 1334 capture–recapture histories. Guanaco population trends in sections with and without roundups were stable throughout a normal-rainfall period and declined during the drought that followed. Roundups were followed by temporary declines in density estimates probably associated with altered guanaco behavior. Tagged guanacos were rarely observed outside the section with roundups and none of the radiocollared guanacos permanently left the section. We estimated a constant annual survival rate for shorn guanacos (82% SE = 0.01) that was independent of sex and age. Yearling proportions declined in the section with roundups 2–3 months after summer roundups. Our results suggest that, under conditions similar to those of our study (i.e. following animal welfare practices in a ranch with moderate livestock densities and sections without livestock), live shearing would not imperil wild guanacos if roundups were conducted in spring and during normal-rainfall periods.

1. Introduction

The guanaco (*Lama guanicoe*) is the most abundant South American camelid, although its abundance and distribution have drastically declined since Europeans arrived on the continent (Raedeke, 1979; Puig, 1995; Baldi et al., 2010). At the present time, more than 70% of remnant guanacos inhabit the Argentinean Patagonia, mainly on private rangelands, where they are persecuted due to competition with livestock, primarily sheep (Rey et al., 2009; Baldi et al., 2010). Guanacos have high quality wool that resembles that of vicuñas (*Vicugna vicugna*), the other wild South American camelid, and can be sold for prices much higher than sheep wool (Sahley et al., 2007; Baldi et al., 2010; Arzamendia and Vilá, 2012). During the last decade live shearing of wild guanacos (Montes et al., 2006; Rey et al., 2009) has been promoted by Patagonian wildlife agencies, such as in the provinces of Chubut, Río Negro, Neuquén and Santa Cruz, as an alternative economic activity for ranch owners and local communities, and as a conservation strategy for wild guanacos (Baldi et al., 2010).

* Corresponding author. Tel.: +54 02972 492797; fax: +54 02972 492471.
E-mail addresses: fitzrey@gmail.com (A. Rey), anovaro@wcs.org (A.J. Novaro), msahores@cedicom.com.ar (M. Sahores), mlguichon@unlu.edu.ar (M.L. Guichón).

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More than 11,000 wild guanacos have been shorn in Patagonia since 2003 (Baldi et al., 2010), based on previous experiences live shearing wild vicuñas (Sahley et al., 2007; Arzamendia and Vilá, 2012). However, the effect of live shearing guanacos on their population dynamics and persistence have not been evaluated.

Live shearing of wild guanacos produces disturbances that may affect individuals, social groups, and populations. Roundup and capture can modify habitat use and produce temporary behavioral alterations in ungulates (Morellet et al., 2009), and cause disruption of vicuña social structures (Sarno et al., 2009). Roundup, restraint and handling increase the risk of capture myopathy that can be lethal for ungulates even 1 month after release (West et al., 2007; Carmanchahi et al., 2011). Energetic costs resulting from live shearing could affect survival and reproduction (Bonacic et al., 2006; Sahley et al., 2007; Arzamendia and Vilá, 2012).

Therefore, we evaluated the effects of live shearing wild guanacos on their movements, survival, recruitment and population trend in a sheep ranch in northern Patagonia. We tested whether guanaco roundups induced movements outside sections with roundups, reduced adult survival and yearling proportions, and resulted in a negative population trend.

2. Methods

2.1. Study area

We conducted our study in the northern Patagonia-province of Río Negro, Argentina, between 2003 and 2009 (Fig. 1). The area is relatively flat and varies in altitude from 400 to 500 m asl. The habitat was characterized by an open shrub steppe with tall and low shrubs, grasses and abundant bare soil. Mean annual temperature was 12 °C and mean annual precipitation was 200 mm during past decades (Paruelo et al., 1998b). A severe drought occurred during our study period, beginning in December 2006. Mean annual precipitation decreased from 237 ± 15 mm/year during 2003–2006 to 110 ± 29 mm/year in 2007–2009.

We worked in three 50–55 km^2-contiguous sections within Cabeza de Vaca ranch (hereafter called CV) (40°S, 66°W), where roundups of guanacos were initiated in 2003. Sections were divided by 0.9–1.15 m-high wire-fences that limited but did not completely restrict guanaco movements (Rey et al., 2012) (Fig. 1a). In section G, where livestock had not grazed since 1987, seven roundups of guanacos occurred between 2003 and 2007. In section GL, where livestock (mainly sheep and a few cattle) regularly grazed, three roundups of guanacos were conducted between 2003 and 2005. In section L, where only sheep regularly grazed, roundups of guanacos were never conducted. Based on differences in guanaco and livestock management we analyzed guanaco population parameters separately for each section and compared them, although some movement of individuals between sections occurred (see movements in results and discussion). All other sections on the study ranch and neighboring ranches had livestock, so we were not able to control the combined effects of livestock grazing and guanaco roundups. Predation on guanacos by puma (*Puma concolor*) was extremely rare during our study because ranch hands killed pumas soon after their tracks were detected (Rey, unpublished data).

2.2. Guanaco roundups and marking

Between 2003 and 2007, the owner of CV ranch conducted 10 guanaco roundups during the austral early spring (September–October) or late summer (February–March) (Table 1). Río Negro wildlife agency staff supervised animal welfare practices. Roundups conducted between 2003 and 2006 ($n = 8$) were aimed at shearing and releasing all guanacos older than 10-months old and extracting yearlings (≤10-months old) for captive breeding (Table 1). Roundups conducted in 2007 ($n = 2$), at the beginning of the drought period, were aimed primarily at extracting adults for a reintroduction program in a national park and yearlings for captive breeding, so few adults were shorn and released (Table 1).

Between 21–33 horsemen herded guanacos over 25 km^2 through a 600-m funnel into a triangular 25–35-ha enclosure and from there into 0.05–0.12-ha corrals (similar to those described by Montes et al., 2006; Rey et al., 2009; Carmanchahi et al., 2011). Ranch personnel immediately separated yearlings in the corral by guiding small groups of guanacos into an adjacent shearing pen where they were blindfolded and restrained by their legs. Up to four guanacos were simultaneously shorn (avoiding neck, belly and tail) with mechanical shears. Just after shearing and before release, we marked guanacos with numbered cattle ear tags and, in most cases, with a colored nylon collar to distinguish sex (Table 1). Additionally we fitted 29 guanacos with radiocollars (Advanced Telemetry Systems) equipped with mortality sensors in the following roundups: 10 shorn adult males in February 2006, five unshorn adult females in March 2007, and seven shorn and seven unshorn adult females in October 2007 (Table 1). Due to small sample sizes, we used telemetry data only to complement data from line-transect and capture–recapture methods (see Sections 2.3 and 2.4). For all tagged guanacos, we registered sex and two age categories (young: 10–22-months old; adults: >22-months old) based on relative size. Shearing and marking of each guanaco took approximately 15 min, and 10 additional minutes to attach radiocollars.

2.3. Guanaco movements and population trends

From January 2003 to March 2009, we estimated guanaco density and population structure through diurnal line-transect surveys on 23 occasions (Table 1). Between 2003 and February 2006, we surveyed guanacos from vehicular or pedestrian line-transects along existing roads, recording the size and perpendicular distance from the road to the detected initial location of each guanaco group (Fig. 1a). Starting in April 2006 we improved our density estimation method by surveying guanacos along regularly-spaced pedestrian line-transects conducted bimonthly (except in winter when they were less frequent) and 2–4 days after roundups. Five to eight transects, 6–9-km long and spaced approximately 1.2 km apart, were surveyed in each section (Fig. 1a), recording guanaco group size, age composition (yearlings ≤10-months old and adults >10-months old; the adult category included young guanacos not reproductively active that could not be distinguished from mature adults at a distance), number of tagged individuals, distance from the observer, and bearing relative to the transect line. During 2006–2009, sections and transects were surveyed in alternate order (day 1: section G transects 1–3; day 2: section L transects 1–3; day 3: section G transects 4–6; and so on) to reduce guanaco disturbance and the likelihood of double-counting groups. All observations were made using Nikon® 12 × 20 binoculars, a Shilba® 20–60 × 80 telescope, a Buschnell® Yardage Pro 1000 laser rangefinder with 1-m precision, and a Suunto® magnetic compass. We interrupted surveys in GL in February 2007 because the ranch owner decided to stop shearing guanacos in that section.

To estimate guanaco densities we used DISTANCE software version 5.0 Release 2 (Thomas et al., 2006), which provided estimates of detection functions based on perpendicular distances from transects and also on distances from the observer and relative bearings to the transect (Buckland et al., 2001). Therefore, we estimated densities that were comparable from surveys conducted throughout the study. We corrected cluster size bias and removed extreme distance values to improve estimations when necessary. To estimate guanaco densities we selected density estimation models using Akaike's Information Criterion (AIC) and goodness of fit tests, and conducted post-stratified analysis for each section and sampling period (Buckland et al., 2001).

To assess short-term effects of roundups on guanaco densities we compared densities 2 months before, 2–4 days after, and 2 months after roundups conducted in February 2006 and March and October 2007. We compared densities within each section using a one-factor ANOVA and t tests with Satterthwaite's approximation (t') when variances were not homogeneous (Caughley and Sinclair, 1994; Buckland et al., 2001).

We used three lines of evidence to evaluate if guanacos left the sections where roundups occurred. First, we assessed the proportion of guanacos that were initially tagged in sections G and GL that were later observed in any of the three sections during the transect surveys. Secondly, we determined whether radiocollared guanacos remained in section G after release and during subsequent roundups. We did this by studying guanaco movements through direct observations and triangulation on non-consecutive days during 10–15-day survey periods every

Table 1
Guanaco roundups and surveys in Cabeza de Vaca ranch.

Date	Section	Captured	Recaptured	Dead	Shorn	Extracted		Released	Marked	
						Adults	Yearlings		Collar-tags	Radiocollars
January-2003					Vehicular transects from roads in G and GL					
September-2003	G	450	0	4	446	0	0	446	222	0
September-2003					Vehicular transects from roads in G					
October-2003	GL	277	0	3	255	0	19	255	254	0
November-2003					Pedestrian transects from roads in GL					
May-2004					Vehicular transects from roads in G, L and GL					
September-2004	G	239	34	3	236	0	0	236	204	0
September-2004	GL	116	26	1	115	0	0	115	89	0
October-2004					Vehicular transects from roads in G, L and GL					
February-2005	G	620	172	5	477	0	138	477	308	0
February-2005					Vehicular transects from roads in G and GL					
September-2005					Vehicular transects from roads in G and GL					
October-2005	GL	29	3	3	26	0	0	26	3	0
October-2005	G	100	51	1	99	0	0	99	49	0
December-2005					Vehicular transects from roads in G and GL					
February-2006	G	772	286	4	732	0	36	732	448	10
February-2006					Vehicular transects from roads in G, L and GL. Telemetry					
April-2006					Pedestrian regularly-spaced transects in G and L. Telemetry					
June-2006					Pedestrian regularly-spaced transects in G and L. Telemetry					
October-2006					Pedestrian regularly-spaced transects in G, L and GL. Telemetry					
December-2006					Pedestrian regularly-spaced transects in G, L and GL. Telemetry					
February-2007					Pedestrian regularly-spaced transects in G, L and GL. Telemetry					
March-2007	G	87	42	0	0	60	21	6	0	5
March-2007					Pedestrian regularly-spaced transects in G, L and GL. Telemetry					
May-2007					Telemetry					
June-2007					Pedestrian regularly-spaced transects in G, and L. Telemetry					
September-2007					Pedestrian regularly-spaced transects in G. Telemetry					
October-2007	G	210	90	0	30	87	0	123	74	14
October-2007					Pedestrian regularly-spaced transects in G and L. Telemetry					
December-2007					Pedestrian regularly-spaced transects in G and L. Telemetry					
February-2008					Pedestrian regularly-spaced transects in G and L. Telemetry					
May-2008					Pedestrian regularly-spaced transects in G and L. Telemetry					
January-2009					Pedestrian regularly-spaced transects in G and L. Telemetry					
March-2009					Pedestrian regularly-spaced transects in G and L. Telemetry					
Total		2900	704	24	2416	147	214	2515	1.651	29

Dates of population surveys and roundups from 2003 to 2009, indicating numbers of guanacos captured, marked, and extracted.

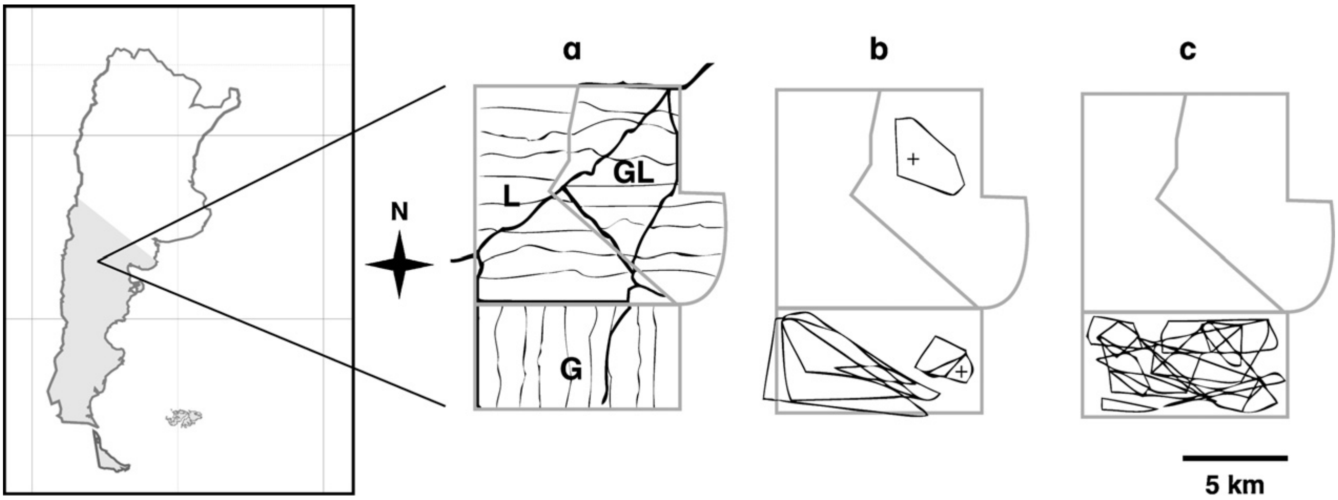

Fig. 1. Location of Cabeza de Vaca ranch in Argentinean Patagonia, surveyed sections and transects, and radiocollared guanacos locations. (a) Three surveyed sections (G, L, GL) showing vehicular (black bold lines) and pedestrian (black thin lines) transects; the sections are divided by wire-fences (gray lines); (b) minimum convex polygons joining locations of six radiocollared males tracked for at least 1 year (+ indicate seasonal locations of the same male); (c) minimum convex polygons joining locations of 13 radiocollared females tracked for at least 1 year.

2 months (same periods when abundance surveys were conducted) and during roundups. We mapped minimum convex polygons based on 217 locations for guanacos tracked longer than 1 year (Kernohan et al., 2001). Finally, we determined the proportion of guanacos tagged that were recaptured in roundups in sections G and GL.

We estimated the finite rates of increase for guanaco populations in each section ($\lambda = e^r$) based on the exponential rate of increase (r) calculated as the slope of the linear regression of the natural logarithms of guanaco population size on time (Caughley and Sinclair, 1994). We estimated population sizes from density estimations and section sizes. To avoid underestimation caused by possible altered behavior produced by roundups we excluded density estimations conducted immediately after roundups (Morellet et al., 2009). As we stopped surveys in GL at the beginning of the drought period, we only estimated population growth in GL during the normal-rainfall period. To estimate livestock density for each section we obtained livestock abundances from the ranch owner that were converted into guanaco units (hereafter called GU) based on forage consumption (sheep = 0.5 GUs; lamb = 0.3; cow = 3) (de Lamo et al., 2001).

2.4. Survival and causes of death of shorn guanacos

We studied survival rates of shorn guanacos via mark-recapture and radiotelemetry. We constructed a capture–recapture matrix using the capture history of 1098 adults (>22-months old) and 236 young (10–22-months old) guanacos that were captured in section G over the course of seven roundups between September 2003 and October 2007 (Table 1). We excluded from the analysis guanacos that were captured and marked in March 2007 ($n = 37$) and yearlings captured in all roundups because they were all removed. We estimated survival probability with program MARK version 5.1 (White and Burnham, 1999), based on the Cormack–Jolly–Seber model (Pollock et al., 1990). We analyzed survival rates for sex and age groups (young and adults) and between roundups, with the following most saturated model: $\{\varphi(\text{group} \times \text{time}),\ p(\text{group} \times \text{time})\}$. We then searched for a reduced model based on the smallest values of Akaike's (1973) Information Criterion ($\text{AIC} = \pm 2 \ln L + 2p$), which combines the lack of fit measured by the log likelihood of the model ($\ln L$) with the number of estimated parameters (p). We selected the most parsimonious model based on the lowest corrected Akaike's Information Criterion (AIC_c), considering two models equivalent when their ΔAIC_c was smaller than 2 (Anderson et al., 1994), and the smallest number of parameters. Program MARK provided monthly estimates of survival rates.

We used survival data from radiocollared guanacos to complement capture–recapture data. We monitored survival of radiocollared guanacos during the 10–15-day-long bimonthly survey periods and during an additional period in May 2007 (Table 1). We estimated approximate date of death and cause of mortality of radiocollared guanacos through observation of carcasses and assessed nutritional condition by visual examination of femoral marrow fat (Caughley and Sinclair, 1994). We estimated survival rate and causes of mortality of radiocollared guanacos throughout the first year after marking using the Kaplan–Meier method, grouping data from different marking events to increase sample sizes.

2.5. Yearling proportions

We studied the effect of roundups on yearling recruitment by assessing changes in proportions of yearlings in sections G and L and proportions of yearlings associated with radiocollared females. We determined proportions of yearlings recorded in G and L in transect surveys during and after breeding seasons from 2005–2006 to 2008–2009. To compare yearling proportions between sections throughout breeding seasons we used a two-way ANOVA in 2006, when transects differed between surveys, and a two-way repeated-measures ANOVA and Tukey's multiple comparison test in 2007 and 2009, when transects were the same in every survey.

We quantified the rates of removal of yearlings and adult females during the February 2006 and March 2007 roundups to assess their potential impact on recruitment. We calculated maximum rates of removal by dividing the number of yearlings plus adult females removed by the number of yearlings that was estimated in G immediately before roundups. Because removal of adult females that had yearlings that were not captured in February and March likely led to death of those yearlings, we assumed conservatively that all adult female removal was equivalent to yearling removal, although some females removed may have not had yearlings.

Additionally, during the 2007–2008 and 2008–2009 breeding seasons we recorded the number of yearlings observed with shorn and unshorn females that were radiocollared in October 2007. We identified mother-yearling associations by assessing female-yearling distances and exclusive interactions.

3. Results

3.1. Guanaco movements and population trends

Guanaco density estimates declined immediately after roundups in February 2006, March 2007 and October 2007 in section G but rebounded to pre-roundup levels in the following 2–3 months (Fig. 2). Surprisingly, similar declines and rebounds occurred in adjacent L and GL sections without roundups (Fig. 2). Density declines and rebounds were not significant ($p > 0.1$) with the exception of the decline after the February 2006 roundup ($F_{2,8} = 6.91$,

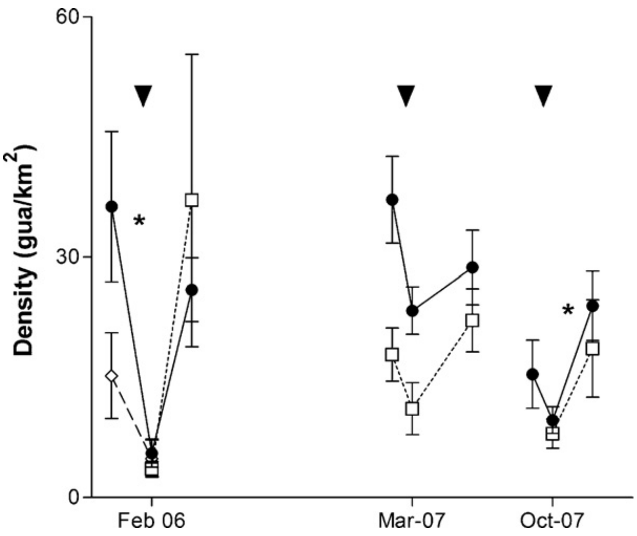

Fig. 2. Guanaco density variation after 2006–2007 roundups in Cabeza de Vaca ranch. Guanaco density and SE in sections: G with guanaco roundups (●), GL with guanaco roundups and livestock grazing (◊), and L with livestock grazing (□). Estimated density before, immediately after, and 2–3 months after roundups in section G (indicated as ▼) are shown.

$p = 0.018$; Tukey test $q = 5.14$, $P < 0.05$) and the increase after the October 2007 roundup ($F_{2,19} = 4.52$, $p = 0.024$; $q = 4.23$, $P < 0.05$) in section G.

We recorded few tagged or radiocollared guanacos outside the section where they were first captured. We never observed tagged guanacos in section L during the 13 surveys between February 2006 and March 2009 (5277 guanacos observed). In contrast, during the same period, we observed an average of 16% tagged guanacos (SE = 0.03; 9014 guanacos observed in 14 surveys) in section G (1334 guanacos tagged in G; Table 1) and 1% tagged (SE = 0.01; 1979 guanacos observed in four surveys) in section GL (317 guanacos tagged in GL; Table 1). Out of 704 recaptures during roundups (Table 1), only 16 recaptures (2.3%) were of guanacos that moved between sections G and GL. One of these recaptures occurred in section GL, 2 days after the guanaco was first captured in section G, whereas the remaining 15 recaptures occurred between 5 and 27 months after the initial capture. Finally, 27 (93%) of 29 radiocollared guanacos were never observed outside section G where they were marked (Fig. 1). None of the six guanacos radiotracked during the March and October 2007 roundups left section G during those roundups. Two radiocollared shorn males were located on 13 occasions in adjacent sections; one intermittently <0.5-km from G, while the other shifted ranges seasonally, being recorded in GL in fall-winter surveys in 2006 and 2007 and returning to G in spring–summer of 2006–2007 and 2007–2008 (Fig. 1b and c). None of the records of these two males that moved outside G were obtained within the 15 days after their release.

Guanaco population trends were stable or slightly increasing in sections with and without roundups during the normal-rainfall period and declined during the drought period (Fig. 3). During the normal-rainfall period, mean guanaco densities were the highest in G, and both in G and L sections mean guanaco density decreased during the drought (Fig. 4). Livestock density was increased during the drought by the ranch owner in the two sections, G and L, where guanacos were more abundant though only in section G total ungulate density decreased (Fig. 4).

3.2. Survival and causes of death of shorn guanacos

The two best survival models that fitted the guanaco capture–recapture data indicated that there were no significant differences in survival rates among sex and age groups (models 1 and 2 in Table 2). Model 2 was preferred because it had fewer parameters (Table 2). The monthly survival rate (0.984 SE = 0.003) estimated from model 2 did not differ significantly between roundups (Table 2). Based on this monthly rate, an annual survival rate of 0.82 (SE = 0.01) was estimated between September 2003 and October 2007,

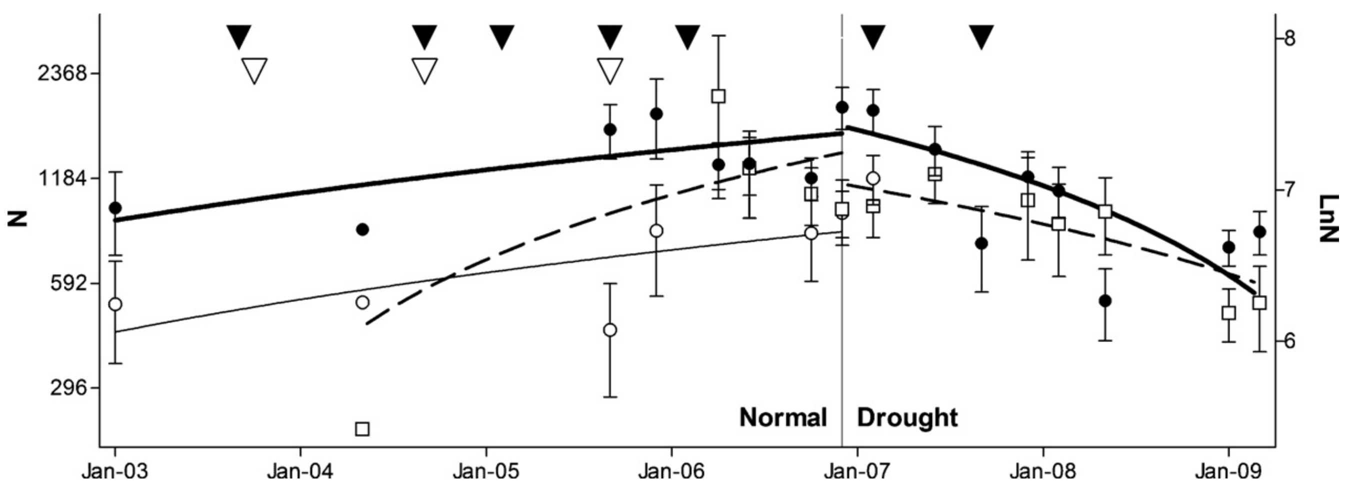

Fig. 3. Guanaco population trends in Cabeza de Vaca ranch from 2003 to 2009. Guanaco population abundances, SE and trends in sections: G with guanaco roundups (● and thick solid line), GL with guanaco roundups and livestock (◊ and dotted line), and L with livestock (□ and thin solid line), before and during the drought period in CV ranch. For June 2004 survey, we were unable to estimate error rates. Lines indicate population trends during the normal-rainfall period ($\lambda_G = 1.01$, $y_G = 6.79 + 0.01x$, $F_{1,6} = 4.92$, $p = 0.07$; $\lambda_{GL} = 1.01$, $y_{GL} = 6.11 + 0.01x$, $F_{1,4} = 3.81$, $p = 0.12$; $\lambda_L = 1.05$, $y_L = 4.7 + 0.05x$, $F_{1,3} = 6.42$, $p = 0.09$) and during the drought period ($\lambda_G = 0.96$, $y'_G = 9.11 - 0.04x$, $F_{1,7} = 9.71$, $p = 0.02$; $\lambda_L = 0.97$, $y'_L = 8.4 - 0.03x$, $F_{1,6} = 12.56$, $p = 0.01$). We indicate dates of roundups in section G (▼) and in GL (▽).

Table 2
Shorn guanaco survival models.

Model	AICc	ΔAICc	Weighted AICc	Model likelihood	Parameters
(1) $\varphi(t)\,p(g\times t)$	3064.69	0	0.49	1.00	29
(2) $\varphi(\cdot)\,p(g\times t)$	3064.91	0.21	0.44	0.90	25
(3) $\varphi(g)\,p(g\times t)$	3068.44	3.74	0.07	0.15	28
(4) $\varphi(g)\,p(t)$	3084.69	19.99	0	0	10
(5) $\varphi(g\times t)\,p(g\times t)$	3085.89	21.20	0	0	42
(6) $\varphi(g\times t)\,p(t)$	3090.40	25.70	0	0	29
(7) $\varphi(t)\,p(t)$	3093.20	28.51	0	0	11
(8) $\varphi(\cdot)\,p(t)$	3093.48	28.78	0	0	7
(9) $\varphi(t)\,p(g)$	3353.47	288.78	0	0	10
(10) $\varphi(g\times t)\,p(g)$	3369.91	305.22	0	0	28
(11) $\varphi(t)\,p(\cdot)$	3369.99	305.30	0	0	7
(12) $\varphi(g\times t)\,p(\cdot)$	3378.52	313.82	0	0	25
(13) $\varphi(\cdot)\,p(g)$	3552.82	488.13	0	0	5
(14) $\varphi(g)\,p(g)$	3553.03	488.34	0	0	8
(15) $\varphi(g)\,p(\cdot)$	3564.49	499.79	0	0	5
(16) $\varphi(\cdot)\,p(\cdot)$	3597.32	532.62	0	0	2

Model selection for Cormack–Jolly–Seber estimates of survival (φ) and recapture probabilities (p) as a function of time (t) and sex-age group (g) for guanacos captured in 2003–2007.

for guanacos shorn up to four times until February 2006 (Table 1).

Annual survival of radiocollared guanacos during the end of the normal-rainfall period and the following drought was 0.68 (SE = 0.08, n = 29), with no significant differences between survival of shorn (φ = 0.70, SE = 0.11, n = 17) and unshorn (φ = 0.58, SE = 0.14, n = 12) guanacos (χ^2 = 0.006, p = 0.94). Highest mortality of radiocollared guanacos was recorded for animals rounded in summer (February 2006 and March 2007) (Fig. 5). Four out of 10 males shorn and radiocollared in February 2006, during the normal-rainfall period, died within the following 2 months after roundup, the period of high risk of capture myopathy (Fig. 5), including one that had been shorn three times during the preceding 13 months. All five unshorn females radiocollared in March 2007, at the beginning of the drought, died before October 2007 but after the period of risk of capture myopathy (Fig. 5). Domestic dogs killed one of these females and the carcasses of the remaining four had soft, pink femoral marrow, indicating starvation as a possible cause of death. Annual survival rates of adult females radiocollared in spring 2007, during the drought, were similar for shorn

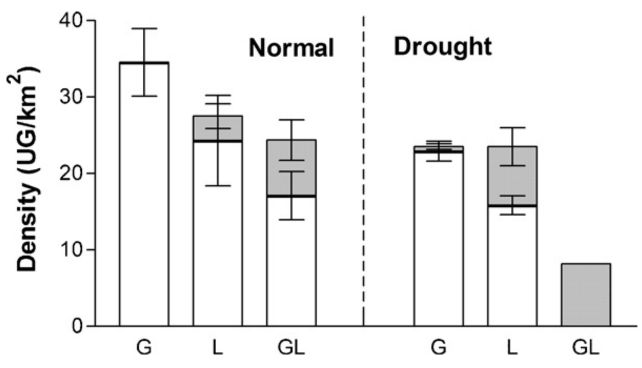

Fig. 4. Guanaco and livestock densities in Cabeza de Vaca ranch during the normal rain-fall and the drought periods. Density of guanacos (white bar) and livestock (in guanaco units, gray bar) and SE per section during the normal (2003–2006) and drought (2007–2009) periods. Guanaco density was not estimated in section GL during the drought.

(φ = 0.86, SE = 0.15, n = 7) and unshorn guanacos (φ = 1, SE = 0.00, n = 7) (χ^2 = 0.001, p = 0.97) and no deaths occurred within the period of risk of capture myopathy (Fig. 5).

3.3. Yearling proportions

The proportion of yearlings was significantly higher in L than in G during both surveys after the February 2006 roundup ($F_{\text{section}\times\text{time }1,22}$ = 0.02, p = 0.89; $F_{\text{section }1,22}$ = 8.92, p = 0.007; $F_{\text{time }1,22}$ = 0.09, p = 0.77) (Fig. 6). The proportion of yearlings differed between sections and surveys conducted before and after the March 2007 roundup ($F_{\text{section}\times\text{time }3,42}$ = 5.00, p = 0.005), although it was significantly higher in L than in G only in the June (early winter) survey (Tukey tests in December, February and March: $P \geq 0.23$; Tukey test in June: q = 7.03, p = 0.01) (Fig. 6). Because the birth season in our study site is concentrated in December (late spring), the apparent increase in the yearling proportion during the 2006–2007 summer surveys (December and February) (Fig. 6) could be due to an increase in yearling detection as a result of growth in body size and increased activity level. We observed no yearlings in any of the surveys during the 2007–2008 breeding season, one year after the drought started (Fig. 6).

Contrary to 2005–2006 and 2006–2007, during the early part of the 2008–2009 breeding season the proportion of yearlings was significantly higher in G than L ($F_{\text{section}\times\text{time }1,14}$ = 0.88, p = 0.36; $F_{\text{section }1,14}$ = 7.76, p = 0.01; $F_{\text{time }1,14}$ = 0.25, p = 0.62) (Fig. 6). The proportion of yearlings in G in March 2009 was 0.226 (SE = 0.029), 65% higher than in February 2007 (0.150; SE = 0.031), whereas the proportion in L was similar between those periods (Fig. 6). These declines and rebounds in yearling proportions in G and L during the first two years of the drought were simultaneous with an approximate 50% reduction in guanaco densities in both sections between February 2007 and March 2009 (from 37.17 SE = 5.41 gua/km^2 to 17.65 SE = 2.39 gua/km^2 in G and from 17.88 SE = 3.32 gua/km^2 to 9.43 SE = 2.59 gua/km^2 in L) and small changes in livestock densities (from

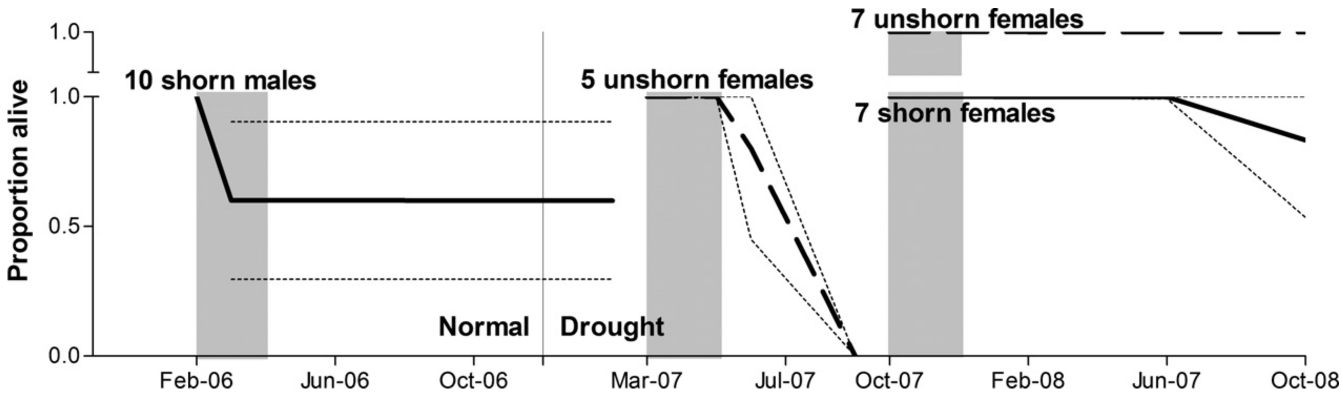

Fig. 5. Survival of radiocollared guanacos marked in Cabeza de Vaca ranch during 2006–2007 roundups. Proportion of alive shorn (thick solid lines) and unshorn (thick interrupted lines) guanacos radiocollared in February 2006, March 2007 and October 2007 roundups and 95% IC (dotted lines). The 2-months periods of high risk of capture myopathy are indicated in gray.

0 UG/km^2 to 0.20 SE = 0.13 UG/km^2 in G and from 6.65 SE = 1.90 UG/km^2 to 8.13 SE = 1.85 UG/km^2 in L).

Yearling removal rate estimated in the February 2006 roundup, when 732 guanacos were shorn, was 0.020 (Table 1) and accounted for 34% of the difference between yearling proportions estimated in G and L in the June 2006 survey (Fig. 6). Yearling removal rate in the March 2007 roundup, when only 87 guanacos were rounded and none were shorn, was 0.033 (Table 1) and accounted for 55% of the difference between yearling proportions in G and L in June 2007 (Fig. 6).

Observation of yearlings in association with females radiocollared in October 2007 resulted in similar patterns to population surveys. Neither shorn nor unshorn radiocollared females were observed with yearlings in the 2007–2008 breeding season, during the early part of the drought. However, both shorn (three out of five) and unshorn (five out of six) radiocollared females were observed with yearlings in the following (2008–2009) breeding season.

4. Discussion

4.1. Guanaco movements and population trends

Roundups did not appear to induce guanaco movements outside the disturbed sections. Location of tagged and radiocollared guanacos in our 6-year study showed that movement away from the 5000-ha section with guanaco roundups was infrequent. Similarly, 93% of wild vicuñas remained within roundup areas (200–400 ha) 1–2 years after live shearing in northern Argentina (Arzamendia and Vilá, 2006, 2012). Declines in guanaco density estimates immediately after the 2006 and 2007 roundups and returns to pre-roundup density levels 2–3 months later may be explained by temporarily altered behavior, as suggested by a relative decline in encounter frequency close to the line transect immediately after roundups (Rey, unpublished data). Altered behavior includes avoidance of humans and reduced activity levels, as has been reported in other ungulates after capture and release events (Morellet et al., 2009), and often results in density underestimation (Buckland et al., 2001). Intense human activities associated with guanaco roundups could also have produced guanaco altered behavior and density underestimation in the contiguous section.

Guanaco population trends were stable or slightly increasing during 4-year normal-rainfall period but declined during the following 2 years of drought. Similar stable or increasing population trends were reported for wild shorn vicuñas during a 3-year period with annual roundups (Arzamendia and Vilá, 2006) and a 5-year period with 4 roundups in Peru (Sahley et al., 2007). Guanaco abundances during the normal-rainfall period in the section with guanaco roundups were among the highest

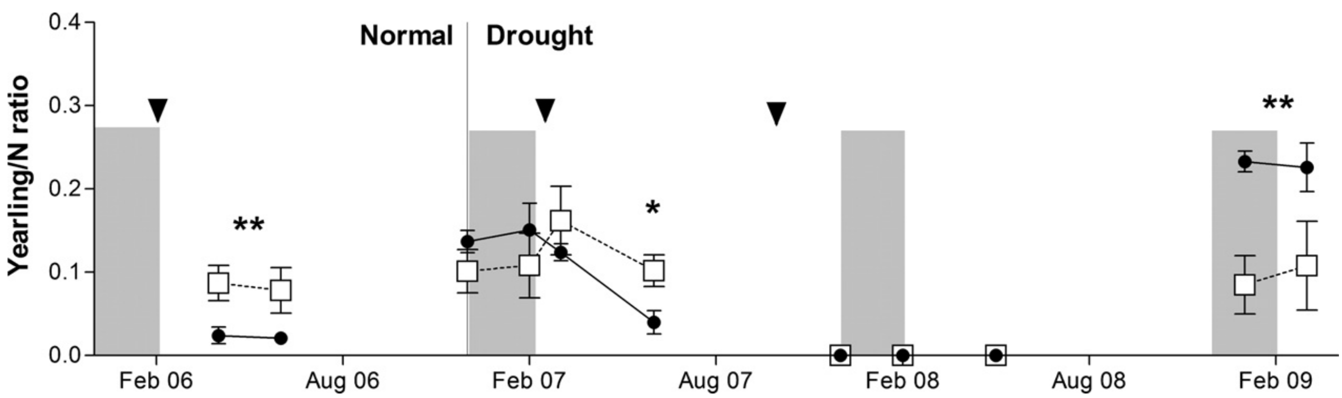

Fig. 6. Yearling proportions from 2006 to 2009 in Cabeza de Vaca ranch. Proportion of yearling/total guanacos in sections G with roundups (●) and L without roundups (□), before and during the drought period. We indicate date of roundups in G (▼) and breeding seasons (gray bars).

reported for Patagonian ranches (Rey et al., 2009; Baldi et al., 2010) and within the carrying capacity range estimated in Patagonia (30–40 gua/km^2) (Puig, 1995). Mean ungulate (guanacos + livestock) abundance also was close to carrying capacity in contiguous sections during the normal-rainfall period. The declining guanaco population trend we observed in sections with and without livestock during the drought could be due to a drastic reduction in food availability. Reductions of this type were also reported for other guanaco populations with no roundups during droughts and severe winters (Raedeke, 1979; Baldi, unpublished data) and other ungulates like gazelle (*Gazella subgutturosa marica*) and Arabian oryx (*Oryx leucoryx*) (Islam et al., 2010; Ismail et al., 2011). The steeper population decline during the drought in the section with guanaco roundups could be explained by the combined effects of guanaco management (which included roundups, capture, shearing and adult removal) and reduced food availability in this period.

4.2. Survival and causes of death of shorn guanacos

Estimated survival rate of shorn guanacos was similar among sex and age groups and between roundup seasons. We expected similar survival rates between sexes in a monomorphic species like guanaco. Conversely, we expected shorn young guanacos (10–22-months old) to have higher mortality than older guanacos, because 1-year old guanacos that are forced to leave family groups may be exposed to higher risks (Sarno et al., 2003). Constant survival rate between roundups suggests similar mortality risks for young and adults when roundups were conducted either before (austral-spring) or after (austral-summer) the breeding season. However, higher mortality of radiocollared shorn guanacos was associated with the summer roundup, mainly during the period of high risk of capture myopathy. This risk could have been increased due to high temperatures during the February 2006 roundup (up to 47 °C) and large and increasing daily thermal amplitude in the following months (Sahley et al., 2007; West et al., 2007). However, a drastic temperature decrease 2 days after the roundup (A.R., personal observation) could also have caused hypothermia of shorn guanacos. This highlights the potential incidence of roundup season that has also been reported in shorn vicuñas (Galaz and Bonacic, 1996).

Compared to unmanaged guanaco populations with no puma predation, our estimation of annual survival of shorn guanacos (82%) was lower than in the Payunia Reserve (88%) (Puig, 1986) and similar to Tierra del Fuego (79%) (Raedeke, 1979). No other study reported survival rates of shorn guanacos. Our 6-month survival rate for guanacos shorn in spring and summer (90.7%) was similar and lower, respectively, to vicuñas shorn only once in spring in Chile (87.1%) (Gimpel and Bonacic, 2006) and Argentina (98%) (Arzamendia and Vilá, 2006, 2012). Our results suggest that roundups did not produce high mortality of shorn guanacos during the normal-rainfall period. Our survival estimation based on mark-recapture, however, did not include the combined effects of shearing and drought because there were no roundups after October 2007. Actually, all deaths of unshorn guanacos radiocollared in March 2007 were likely related to starvation, which was the main cause of death in other ungulate populations during droughts (Islam et al., 2010; Baldi, unpublished data). Low mortality of shorn and unshorn guanacos after the October 2007 roundup (1 out of 14 radiocollared guanacos), on the other hand, suggests that favorable climate conditions and high food availability in spring could reduce mortality even during droughts.

4.3. Yearling proportions

Similarly to other guanaco populations (Baldi, personal communication) and other ungulates like Arabian oryx (Ismail et al., 2011), the drought in our study had a dramatic effect on birth rates and/or yearling survival, thus affecting yearling proportions, during the 2007–2008 breeding season. However, 1 year later the proportion of yearlings in the section with guanaco roundups was the highest recorded throughout the study and among the highest reported for this species (8–30% [cited in Saba et al., 1995]). Rebounding in the section with guanaco roundups after >1 year without roundups and a failed breeding season could have been favored by the lack of livestock. Accordingly, 2 years into the drought, both shorn and unshorn radiocollared females produced yearlings, as reported for shorn and control vicuñas in Argentina and Peru (Arzamendia and Vilá, 2006; Sahley et al., 2007). Before the drought, yearling proportions after late summer (postpartum) roundups were lower in the section where guanaco roundups occurred. The reduction in yearling proportion 3 months after the March 2007 roundup exceeded the extraction of yearlings conducted in that management event and could be associated with starvation of 2–3-month-old yearlings separated from their mothers.

5. Conclusions

Live shearing conducted following strict welfare guidelines in our study area did not imperil the guanaco population during the normal-rainfall period and might contribute to its conservation in a region where guanacos are otherwise heavily persecuted and replaced by livestock. However, guanaco shearing should be avoided during droughts. Factors such as wire-fences and high livestock numbers, that are common in Patagonian ranches, may exacerbate the negative effects of roundup and shearing during adverse climatic conditions. To avoid affecting recruitment and allow more time for recovery before winter, roundups should only be conducted in spring (i.e. before parturition). Long-term studies of social and demographic effects of guanaco live shearing under different environmental conditions are necessary to develop adaptive strategies so that management of wild guanaco populations can contribute to their conservation.

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