

Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population

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Neotropical ungulates are poorly understood with regard to age-specific mortality and how it relates to different mortality causes. During January 2008–April 2011, we investigated mortality patterns of calf (<1 year old) and adult vicuñas (*Vicugna vicugna*) in west-central Argentina. Specifically, we analyzed whether birth mass, birth date, and sex of radiomarked vicuña calves affected 1st-year survival; quantified cause of death for marked calves and unmarked adults; and explored how primary productivity and quality of forage and diet related to body condition of adult vicuña carcasses. Birth mass was a strong predictor of 1st-year survival: a 1-kg (~18%) increase in birth mass resulted in a 54% decline in the risk of death. Further, low survival rate in 1 calendar year was associated with low mean birth mass during that year, but not with population density and forage quality in the previous year. Puma (*Puma concolor*) predation accounted for $\geq 49\%$ ($n = 93$) and 91% ($n = 89$) of the mortality in calves and adults, respectively. Body condition of adult vicuñas killed by pumas varied seasonally and correlated with seasonal changes in primary productivity and forage and diet quality. Our results highlighted the importance of puma predation and low birth mass as proximate causes of vicuña mortality. How environmental factors (e.g., early summer precipitation) influence forage and ultimately mortality has yet to be determined.

Key words: birth mass, body condition, predation, puma, South America, vicuña

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Knowledge of how food and predators influence mortality is key to the processes that determine ungulate numbers. For instance, decreasing forage quality and availability predispose malnourished individuals to starvation (e.g., Mduma et al. 1999; Sinclair 1977; Singer et al. 1989) and predation (e.g., Mech et al. 1995; Pole et al. 2004; Wright et al. 2006). Furthermore, forage shortage depresses pregnancy rates (e.g., Cook et al. 2004; Stewart et al. 2005) and birth mass (e.g., Rognum et al. 1982; Thorne et al. 1976), which ultimately affect recruitment (Côté and Festa-Bianchet 2001).

Food and predators differentially affect discrete aspects of ungulate populations. Losses to malnutrition typically affect young and old animals more than others (reviewed by Gaillard et al. 2000), and males more than females in sexually dimorphic ungulate species (Clutton-Brock et al. 1982; Owen-Smith 1993). Losses to predation depend on the interaction between individual traits of the prey and the hunting mode of the predator. Cursorial and ambush predators tend to select young and old individuals (Hornocker 1970;

Mech et al. 1995; Pierce et al. 2000), especially when preying upon large ungulates (reviewed by Temple 1987). However, ambush predators may kill prime individuals if prey occur in groups and the success of the attack depends on proximity rather than prey characteristics (Logan and Sweaner 2001).

Vicuñas (*Vicugna vicugna*) are medium-sized (38–40 kg), group-living ungulates that inhabit high deserts (3,200–4,800 m elevation) of the puna ecosystem in the Andes of South America (Franklin 2011). Vicuñas are the most abundant native large herbivore of the puna, yet information on mortality factors in their populations is scarce. In 1 Peruvian population, exposure, lightning, calf losses to culpeo foxes (*Lycalopex culpaeus*), and predation on adults from unknown agents explained natural mortality (Franklin 1982; Hofmann et al. 1983). Earlier studies conducted at San Guillermo National



Park, Argentina, reported that winter losses resulted from winter kill and puma (*Puma concolor*) predation, but the cause of 45% of deaths was unknown (Cajal and Lopez 1987). To date, the relative importance of various mortality causes, timing of deaths, and factors that influence the extent of vicuña losses are mostly unknown.

Here, we quantify mortality patterns in a vicuña population under puma predation during a 3.4-year period. Specifically, we investigated the effects of birth mass, birth date, and sex on 1st-year mortality of vicuña calves; causes, extent, and seasonal timing of mortality in calves and adults; and how changes in diet quality and primary productivity related to body condition and mortality patterns of vicuñas.

MATERIALS AND METHODS

Study area.—We conducted this study at San Guillermo National Park during January 2008–April 2011. Located in the central Andes of Argentina (29°14'S, 69°21'W), San Guillermo National Park protects 166,000 ha of semiarid landscapes at 2,000- to 5,600-m elevation (Fig. 1).

Precipitation is scarce (annual \bar{X} = 240 mm) and occurs mainly in summer (December–March) as rain, and winter (May–September) as snow. January is the warmest month (\bar{X} = 14°C), whereas July is the coldest (\bar{X} = –1°C). The annual temperature ranges from –23°C to 27°C (Salvioli 2007). Warmer temperatures and occasional rains allow a pulse of plant growth during January–March. Low temperatures and water limitation characterize the nongrowing season in the remaining months (Hofmann et al. 1983).

Extensive open plains (~3,400 m in elevation) surrounded by hills and mountain peaks characterize the landscape. Narrow canyons (20–300 m wide) with steep, rocky walls dissect the plains and mountains. Isolated patches of meadows are located in the plains or along rivers and streams. Vegetation in plains and canyons is characterized by a shortgrass steppe dominated by perennial grasses (*Jarava* spp. and *Stipa* spp.) and scattered shrubs (*Adesmia* spp.); in canyons, other shrubs such as *Lycium chanan* and *Larrea divaricata* are common. In meadows, dominant plants include sedges (*Carex* spp. and

Scirpus spp.), rushes (*Juncus* spp.), and fescues (*Festuca* spp.—Martínez Carretero et al. 2007). High vegetation cover (\bar{X} = 75% [95% confidence interval {95% CI} = 66–83%]) and relatively tall grasses in meadows (height \bar{X} = 19 cm [95% CI = 16–21 cm]), and shrubs and rocky outcrops in canyons favor the ambush hunting style of pumas (Cajal and Lopez 1987).

The park harbors a nearly intact community of native vertebrate species, including populations of vicuñas and guanacos (*Lama guanicoe*). Recent surveys suggest that vicuña density increased 10 times in the last ~27 years (density estimate for 2007 ~ 8.5 individuals/km²) and is 10 times greater than that of guanacos (Puig and Videla 2007). At San Guillermo National Park, 83% of vicuña calves are born during the last 3 weeks of January (Ruiz Blanco et al. 2011). Pumas are the only effective predator of vicuñas in the area, sufficiently abundant that pumas were observed 1–3 times per month incidentally to field activities. Other mammalian predators present are culpeo and chilla (*Lycalopex griseus*) foxes, and colocolo (*Leopardus colocolo*) and Andean (*L. jacobitus*) cats; culpeo foxes rarely preyed on vicuña calves (Hofmann et al. 1983).

Capture and handling of calves.—During January 2008–2010, we hand-captured, weighed (to 0.2 kg), and sexed 93 vicuña calves ~ 12 min old (Donadio et al. 2012). We fitted each individual with an ear-tag transmitter (model 3430; Advanced Telemetry Systems, Isanti, Minnesota) that weighed 18 g and consisted of a motion-sensitive transmitter mounted on a plastic tag. Capture and handling procedures followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Calf monitoring, survival, and mortality factors.—We used handheld yagi and omnidirectional whip antennas and receivers (model FM-100; Advanced Telemetry Systems) to monitor marked calves for 1 year. All individuals were monitored daily until 60 days old, and ≥4 times per week thereafter. Mortality events were indicated by changes in the pulse rate of transmitters, which doubled if motionless for >2 h. We investigated all telemetry-signaled deaths as soon as detected. We conducted field necropsies and classified proximate cause of death as puma predation, if we found clear signs that a puma killed the animal (e.g., puma tracks, carcass remains covered with gravel or grass, canine punctures in hide or skull, dragging marks, and broken and chewed large bones and ribs [Sarno et al. 1999]); and nonpredation, if the carcass was intact and no signs of pumas were found. If we could not attribute death to either of the 2 above-mentioned categories, we recorded cause of death as unknown. Examples of the latter cases typically involved finding only a radiotag and a few scattered remains.

Despite our monitoring effort, 7 deaths went undetected for 8–62 days. In these cases, we estimated date of death as the midpoint between the last live and 1st mortality signal. One individual was last located 7 days before it turned 1 year of age; we assumed it was alive at the end of the study period. Three individuals were censored in 2009 at 30, 49, and 63 days

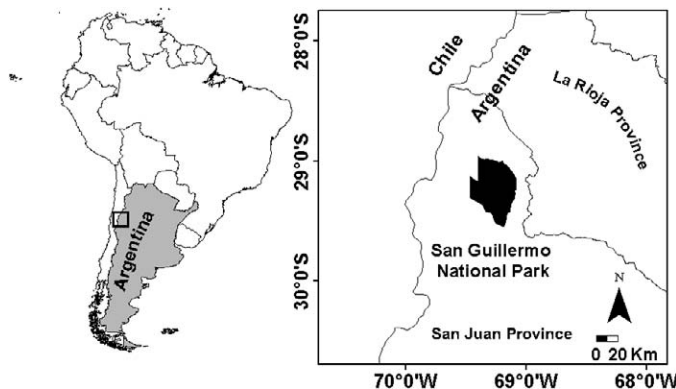


FIG. 1.—Study area location, showing San Guillermo National Park, San Juan Province, Argentina.

of age because of loss of signal ($n = 1$) or transmitters that fell off ($n = 2$).

Normalized difference vegetation index.—We used the normalized difference vegetation index to assess seasonal changes in primary productivity (Kerr and Ostrovsky 2003). We obtained MODIS normalized difference vegetation index 16-day composite grid data (MOD13Q1; temporal resolution = 16 days; spatial resolution = 250×250 m; sinusoidal projection) in HDF format from Earth Observing System Data and Information System (EOSDIS 2009) for the period 1 January 2008–8 May 2011. We used the MODIS Reprojection Tool 4.1 (National Aeronautics and Space Administration 2011) to subset the images to the study area (upper left corner = $28^{\circ}56'S$, $69^{\circ}31'W$; lower right corner = $29^{\circ}34'S$, $68^{\circ}58'W$) and to reproject the data from a sinusoidal to a WGS-84 projection using a bilinear resampling routine. We digitized polygons representing plains and meadows within the study area and estimated normalized difference vegetation index statistics for each habitat type using the Zonal Statistics tool in ArcGIS 10 (ESRI 2011).

Analysis of yearling and adult mortality through carcasses.—We located carcasses of unmarked vicuñas > 1 year old either by direct observation or by investigating sites where avian scavengers were observed. Time since death was estimated based on our frequent surveys of the study area. If a carcass was observed where none had been seen in a previous survey, we assumed that the animal was killed midway between the last time we surveyed the area and the day we found it. We performed on-site necropsies on all carcasses found; proximate causes of death were classified as for calves. If a mandible was present, we assigned the carcass to 1 of 3 age classes based on tooth eruption and wear patterns (Wheeler 1982): yearlings (12–24 months old), adult (24–108 months old), and old adult (≥ 108 months old). Whenever possible, the sex of carcasses was determined based on either genitalia or morphology of the pelvic girdle (Raedeke 1979). We also recorded habitat type (plain, meadow, or canyon) where individuals were killed. If dragging marks were absent, we assumed the animal had been killed where we found it; otherwise, we followed dragging marks to their origin.

Body condition.—We used fat deposits in femur marrow to evaluate body condition of vicuñas during an annual cycle. We used 2 methods to determine body condition. First, we visually inspected in the field a cross section of 1 of the femurs and qualitatively assessed the consistency and color of the marrow. Vicuñas with red or pink bone marrow with a gelatinous consistency were categorized as in poor body condition; those with white or yellowish bone marrows with a solid consistency were categorized as in good body condition (Sinclair and Duncan 1972). For each carcass, the remaining femur was labeled and frozen for further analysis.

Second, we estimated percent weight of marrow fat in 6-cm-long cross sections from midshaft frozen femurs. We extracted and weighed the wet marrow sample from femur segments, then dried it at $50^{\circ}C$ for 2–4 days until the weight stabilized.

Percent fat estimates for each sample were obtained by dry weight/wet weight $\times 100$ (Neiland 1970).

Of 63 femurs collected, 30 dehydrated before collection. To avoid overestimation of percent fat in these specimens, we used marrow samples from nondehydrated femurs (i.e., were 100% filled) to develop an equation relating percent fat and actual amount of fat (g/cm^3 —Peterson et al. 1982). Best fit for the data was a quadratic model: $y = -7.11 + 200.63x - 97.2x^2$, where y was percent fat and x was amount of fat. The model was obtained by centering and scaling the predictor variables and back-transforming the resulting parameter estimates. Nonscaled x_i (amount of fat) values from dehydrated specimens were then inserted into the equation to estimate percent fat. Standard diagnostic tests showed that the model appropriately described the data, assumptions were met, and influential observations and multicollinearity were not present (Kutner et al. 2004).

Forage and diet quality.—We analyzed nitrogen content (Göering and van Soest method—Haufler and Servello 1996) in plants and fecal pellets to evaluate annual (only pellets [i.e., diet quality]) and seasonal changes in forage and diet quality of vicuñas. In San Guillermo National Park, *Jarava* spp., *Stipa* spp., *Festuca* spp., and *Juncus* spp. have been reported as important foods of vicuñas (Cajal 1989); we sampled these plants during January–March and July–December, in 2008–2010. Plants adjacent to vehicle transects were clipped at 1 cm above ground level; distance between sampling locations was 500 m. Samples were stored in paper bags, dried at room temperature (25 – $38^{\circ}C$) for 2–7 days, and frozen until analyzed at the Laboratorio de Evaluación de Forrajes (Instituto Nacional de Tecnología Agropecuaria, Bariloche, Río Negro Province, Argentina).

We collected samples of fresh (black in color and damp) fecal pellets from vicuña latrines adjacent to permanent vehicle transects. Only 1 sample was collected from each latrine to avoid pseudoreplication. Each sample consisted of 30 pellets that belonged to the same aggregation (i.e., they were found in 1 fecal bolus) to ensure that all pellets came from the same individual. Sampling periods, distance between sampling locations, storage, and analytical procedures were similar to those described for plants.

Vicuña density.—In 2008–2009, we surveyed during daylight hours (1000–1400 h) 3 permanent transects (lengths: 10.2 km, 4.9 km, and 13.4 km) from a vehicle with 2 observers standing in the back. We surveyed each transect 3 times in February (summer), May (fall), July–September (winter), and November (spring). Surveys of the same transect were never repeated on consecutive days. For every group of animals encountered, we recorded number of individuals and the perpendicular distance (Bushnell Pro 1000 Rangefinder, Bushnell Corporation, Overland Park, Kansas) from the center of the group to the transect. We used program Distance 6.0 release 2 to estimate annual densities and associated asymmetric 95% CI (Thomas et al. 2010). Transects were not randomly located; thus, resulting density

TABLE 1.—First-year survival estimates and birth masses of vicuña calves at San Guillermo National Park, Argentina, January 2008–January 2011.

Year	Overall survival rates and birth masses				Survival rates and birth masses by sex				
	\hat{S}_{365} (95% CI)	<i>N</i>	Mean weight (95% CI) (kg)	<i>n</i> ^a	Sex	\hat{S}_{365} (95% CI)	<i>n</i> ^a	Mean weight (95% CI) (kg)	<i>n</i> ^a
2009	0.640 (0.514–0.799)	45	5.5 (5.2–5.7)	42	Females	0.563 (0.365–0.867)	16	5.5 (5.1–5.9)	15
					Males	0.660 (0.501–0.869)	27	5.4 (5.1–5.8)	27
2010	0.732 (0.608–0.881)	41	6.1 (5.9–6.2)	39	Females	0.778 (0.608–0.996)	18	6.0 (5.7–6.3)	16
					Males	0.682 (0.513–0.907)	22	6.1 (5.8–6.4)	22
All years ^b	0.661 (0.571–0.766)	93	5.7 (5.5–5.9)	88	Females	0.667 (0.529–0.840)	36	5.7 (5.4–6.0)	33
					Males	0.630 (0.510–0.778)	53	5.7 (5.5–6.0)	53

^a Differences between total number of monitored individuals and number of individuals sexed and weighed resulted from personnel releasing some calves before sexing or weighing them due to maternal aggressiveness.

^b Includes 7 individuals from 2008.

estimates were appropriate only for the purpose of across-year comparisons.

Statistical analysis.—We estimated 1st-year survival functions of marked vicuñas using the Kaplan–Meier product limit estimator (Winterstein et al. 2001). We compared survival functions between sexes and between years (2009 versus 2010). Sex hazard functions had a constant ratio in time and were compared using the log-rank test. Annual hazard functions were not proportional and visual inspection of survival curves showed that they diverged during the 1st weeks of life. Therefore, we compared annual survival functions using the Peto and Peto test, which is more likely to detect differences in survival curves that diverge early (Mills 2011). We used a Cox proportional hazard model (Winterstein et al. 2001) to assess the effect of different covariates (birth mass, birth date, year, and sex) on neonatal survival from birth to 365 days of age. To identify those covariates that could be included in the linear component of the final model, we fitted models that contained each of the covariates 1 at a time (Collet 1999). Only covariates with $P < 0.25$ were selected (Mills 2011).

Covariates birth mass, birth date, and year met the selection criteria. Subsequent fitting of the model showed a significant effect of birth mass ($P = 0.003$), but no effect of birth date ($P = 0.8$) and year ($P = 0.8$) on survival. Furthermore, testing of the proportional hazard assumption showed that it was violated. So, we stratified the model by year, allowing each year to have different baseline hazard functions. Such stratification resulted in a model that met the assumption of proportional hazards and permitted the analysis of the covariate that had a significant effect on survival.

In ungulates, the influence of birth mass on survival may be important during the first days after birth, but decline thereafter (Clutton-Brock et al. 1982; Thorne et al. 1976). We explored this potential time-dependent effect of birth mass by splitting the data into 2 time intervals (≤ 7 and > 7 days old) and using heaviside functions (hv—Kleinbaum and Klein 2011; Mills 2011). We chose 7 days as a cutoff point because one-third of 1st-year mortality occurred during the 1st week of life. We created the covariates hv₁ and hv₂ represented by the interaction between birth mass and the dummy variables g₁(t) and g₂(t), where g₁ equaled 1 if an individual died when ≤ 7

days old or 0 otherwise, and g₂ equaled 1 if an individual died when > 7 days old or 0 otherwise. All survival analyses were conducted using package survival (Therneau and Lumley 2011) in program R 2.13.1 (R Development Core Team 2011).

For statistical analysis, data on body condition were combined into bimonthly intervals, age classes, and sexes. Because of small sample sizes, data on forage quality obtained from plants were pooled for the growing and nongrowing seasons. Diet quality data from fecal pellets were analyzed on a monthly basis. Normalized difference vegetation index data are presented as monthly mean values (95% CI) estimated from all normalized difference vegetation index averages obtained for a given month across all years.

We used analysis of variance (ANOVA) and *t*-tests to analyze data on birth mass of calves, percent fat, and diet quality. Significant ANOVA results ($\alpha = 0.05$) were followed by Tukey's tests for pairwise differences between bimonthly intervals (percent fat) and months (diet quality). Assumptions of normal distribution and equal variances were tested using Anderson–Darling's and Levene's tests, respectively. Failure to meet the assumptions was followed by an arcsine square-root transformation of the data. If after transformation the assumptions were still not met, we used Kruskal–Wallis and Mann–Whitney nonparametric tests; in these cases data are described by their medians, and 1st and 3rd quantiles (Q₁–Q₃). Frequency distributions were compared using chi-square tests, unless expected values were ≤ 4 ; then, we used the Fisher exact test. We used the Pearson's product-moment statistic (*r*) to assess the relationship between bimonthly mean percent fat and percent individuals categorized as in good body condition. Statistical analyses were conducted using Minitab 16 statistical software (Minitab, Inc. 2010).

RESULTS

Calves birth mass, survival, and mortality factors.—Vicuña birth mass was similar between sexes across years ([2009 versus 2010]: $F_{1,76} = 0.003$, $P = 0.95$). Conversely, there was a significant effect of year on birth mass ($F_{1,76} = 11.9$, $P = 0.001$); calves born in 2010 were 11% heavier than in 2009 (Table 1).

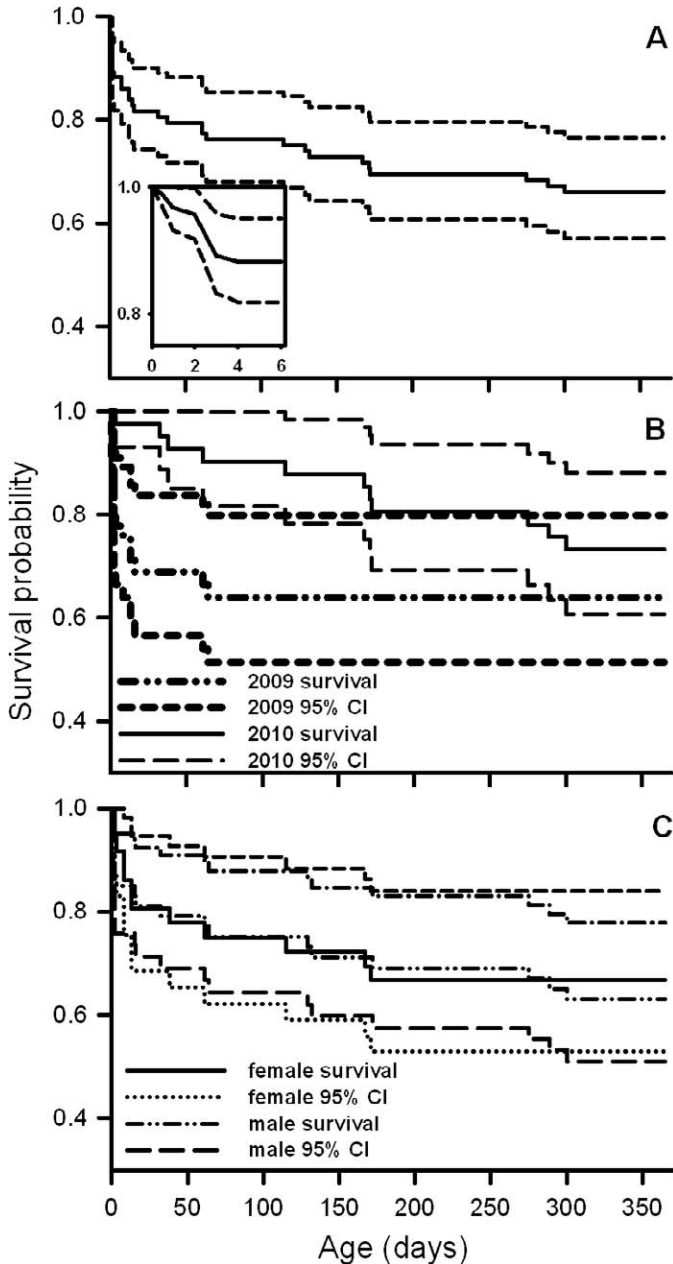


FIG. 2.—First year Kaplan–Meier survival estimates of vicuña calves at San Guillermo National Park, January 2008–January 2011. A) Overall survival (including 7 individuals from 2008); the inset shows the steep decline in survival during the 1st week of life. B) Survival by cohort, only individuals from 2009 and 2010. C) Survival by sex, all years pooled. Samples sizes are reported in Table 1.

We estimated 1st-year survival for 93 ear-tagged calves (53 males, 36 females, and 4 of unknown sex; Table 1). Survival rates were similar between sexes (log-rank, $\chi^2_1 = 0.1$, $P = 0.77$) and 14% higher in 2010 than 2009 (Peto and Peto, $\chi^2 = 2.8$, $P = 0.097$; Table 1). Annual survival curves differed mainly during the early stages of life; this difference was particularly striking during the first 4 weeks, when survival was $\sim 42\%$ higher in 2010 than 2009 (Fig. 2). Small sample size ($n = 7$) precluded a similar analysis for 2008.

TABLE 2.—Cox proportional hazard models (PH Cox) and estimated parameters relating different covariates to vicuña calf survival at San Guillermo National Park, Argentina, January 2008–January 2011.

Model	Parameter	B	$SE(\beta)$	Z	$P(> z)$	Risk ratio [exp(β)]
PH Cox ^a	BM	-0.773	0.269	-2.866	0.004	0.462
Extended PH Cox ^b	hv ₁	-0.543	0.285	-1.905	0.057	0.581
	hv ₂	-1.023	0.296	-3.456	0.001	0.360

^a Model: $h(t,x) = h_0(t) \exp[\beta_1(BM)]$, where h = hazard function, h_0 = baseline hazard function, and BM = birth mass (kg). Likelihood ratio test: $\chi^2_1 = 8.5$, $P < 0.003$, $n = 81$, events (deaths) = 26.

^b Model: $h(t,x) = h_0(t) \exp[\beta_1(hv_1) + \beta_2(hv_2)]$, where $hv_1 = BM \times g_1(t)$ and $hv_2 = BM \times g_2(t)$, and g_1 and g_2 represent 0–7 and 8–365 days-old intervals, respectively. Likelihood ratio test: $\chi^2_2 = 18.1$, $P < 0.001$, $n = 151$, events (deaths) = 26.

Birth mass was the single most important covariate affecting 1st-year survival. A 1-kg increase in birth mass resulted in a 54% decline in the risk of death. However, the extended Cox proportional hazard model showed that this effect declined with time. For individuals older than 7 days of age, the effect of birth mass on risk of death significantly decreased by 64%; in other words, the advantage provided by a higher birth mass faded with time (Table 2).

Puma predation was the primary cause of death (49% of total mortality; $n = 31$) of ear-tagged vicuña calves, followed by unknown causes (32%) and nonpredation (19%). Specific nonpredation factors were difficult to assess in the field with the exception of an individual that died 5 h after birth from a broken leg and associated bleeding.

Cause of mortality varied with time, with nonpredation factors dominating (45%) during the 1st week of life and puma predation being most important (65%) throughout the rest of the 1st year (Fisher exact test, $P = 0.005$; Table 3). Puma predation affected males ($n = 8$) and females ($n = 7$) according to their representation in the marked population ($\chi^2_1 = 0.28$, $P = 0.60$).

Normalized difference vegetation index.—The normalized difference vegetation index showed a consistent seasonal pattern in primary productivity across years and habitats. The index increased in December–April, when it reached its maximum value, and decreased in May–August maintaining afterward constant low values until December (Fig. 3A).

Analysis of yearling and adult mortality through carcasses.—We collected a total of 89 carcasses during January 2008–April 2011. Time since death was <3 days for 69%, 4–7 days for 18%, 8–15 days for 2%, and 20–30 days for 11% of the individuals. Of the carcasses found, 91% showed evidence of puma predation, 5% died from unknown causes, and 3% died due to nonpredation causes, including probable starvation ($n = 2$) and complications during labor ($n = 1$). Individuals with signs of puma predation were found all year-round, and those dying of apparent starvation were found only in early January. Of the 81 individuals killed by pumas, 31% were females, 26% were males, and 43% were unknown, whereas 21% were yearlings, 63% were adults, 10% were old adults, and 6% were of unknown age.

TABLE 3.—Causes of mortality of radiomarked vicuña calves at San Guillermo National Park, Argentina, January 2008–January 2011.

Year	Days since birth			
	1–7	8–14	15–21	22–365
2009				
No. calves	45	35	32	31
No. deaths	10	3	1	2
Cause-specific mortality				
% Nonpredation (<i>n</i>)	40 (4)	33 (1)	0	0
% Puma (<i>n</i>)	20 (2)	33 (1)	100 (1)	50 (1)
% Unknown (<i>n</i>)	40 (4)	33 (1)	0	50 (1)
2010				
No. calves	41	40	40	40
No. deaths	1	0	0	10
Cause-specific mortality				
% Nonpredation (<i>n</i>)	100 (1)	0	0	0
% Puma (<i>n</i>)	0	0	0	80 (8)
% Unknown (<i>n</i>)	0	0	0	20 (2)
Total^a				
No. calves	93	82	78	76
No. deaths	11	4	2	14
Cause-specific mortality				
% Nonpredation (<i>n</i>)	45 (5)	25 (1)	0	0
% Puma (<i>n</i>)	18 (2)	50 (2)	100 (2)	64 (9)
% Unknown (<i>n</i>)	36 (4)	25 (1)	0	36 (5)

^a Includes 7 individuals from 2008.

Body condition.—Fat content in bone marrow of vicuñas killed by pumas varied significantly among bimonthly intervals ($F_{5,53} = 6.40, P < 0.001, n = 59$) and was positively correlated with the mean proportion of individuals in good condition according to visual inspection of bone marrow ($r = 0.97$ [95% CI = 0.74–0.99], $t_4 = 8.0, P = 0.001$). Vicuñas were in better body condition in February–September (midsummer–late winter) than in October–January (early spring–early summer; Fig. 3B).

In both midsummer–late winter ($t_{23} = 1.41, P = 0.086$) and early spring–early summer ($t_{26} = 2.25, P = 0.017$) percent fat of carcasses tended to be lower in canyons and meadows (both habitats combined [$\bar{X} \pm SE$]: midsummer–late winter = 63.7% \pm 16.0%, $n = 7$; early spring–early summer = 15.7% \pm 6.1%, $n = 13$) than in plains (midsummer–late winter = 81.9% \pm 5.4%, $n = 18$; early spring–early summer = 41.8% \pm 9.4%, $n = 15$). Vicuña carcasses in poor body condition tended to be more frequent in canyons and meadows (67% of 21 carcasses found in these habitats) than in plains (37% of 32; $\chi^2_2 = 4.3, P = 0.07, n = 53$), but this trend faded when controlling by season (midsummer–late winter [canyons and meadows = 29% of 7; plains = 17% of 18]: Fisher exact test, $P = 0.44$; early spring–early summer [canyons and meadows = 86% of 14; plains = 64% of 14]: Fisher exact test, $P = 0.19$).

Percent fat was similar ($t_{37} = 0.43, P = 0.67$) between males ($\bar{X} \pm SE = 57\% \pm 8.7\%, n = 18$) and females ($52\% \pm 8.7\%, n = 22$). Also, the frequency of occurrence of individuals in poor ($n_{\text{♀}} = 10, n_{\text{♂}} = 8$) and good ($n_{\text{♀}} = 12, n_{\text{♂}} = 9$) condition was similar between sexes ($\chi^2_1 = 0.05, P = 0.82$). Yearlings (median [Q₁–Q₃] = 92.5 [45.1–98.9], $n = 9$) and adults (68.9 [13.3–92.3], $n = 41$) tended to present higher percent fat values than old adults (25.8 [5.4–82.2], $n = 9$; Kruskal–Wallis $H = 5.97, P = 0.051$). Frequency of occurrence of individuals in

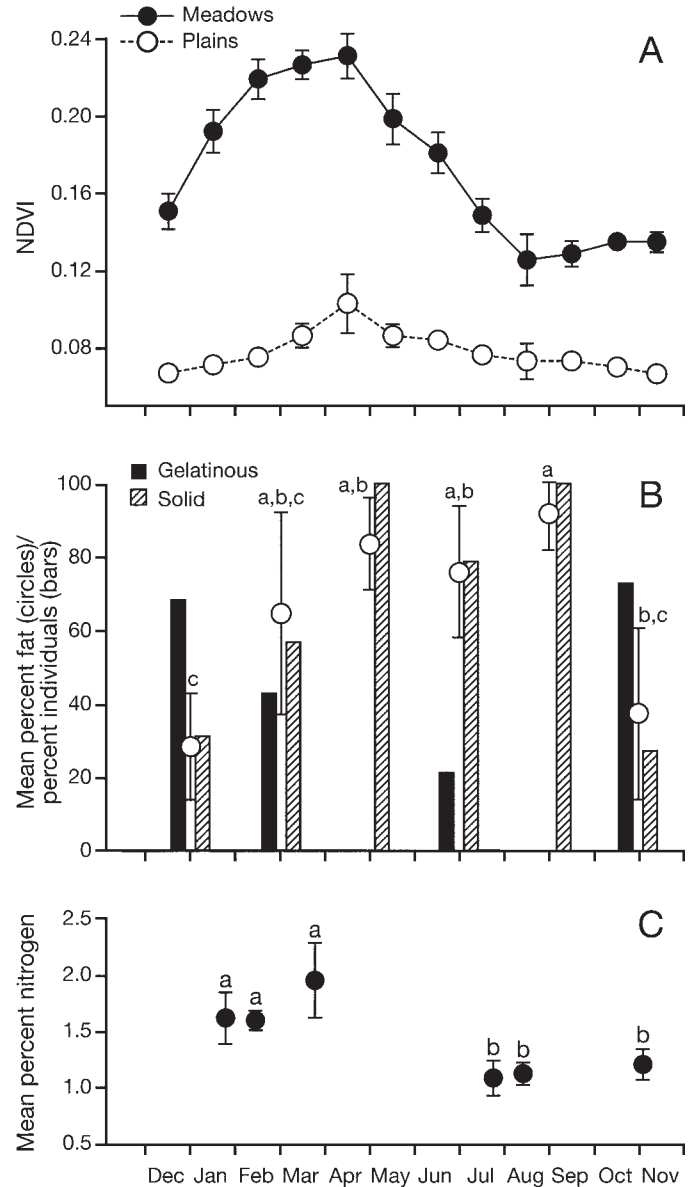


FIG. 3.—Seasonal fluctuations in normalized difference vegetation index (NDVI) values, vicuña body condition, and vicuña diet quality at San Guillermo National Park, Argentina, January 2008–April 2011. A) Monthly means (95% CI) of normalized difference vegetation index values obtained by combining monthly data across years (sample size range: 4–8). B) Mean bimonthly percent fat (95% CI) and percent of individuals in poor and good condition killed by pumas; samples sizes were December–January = 19, February–March = 7, April–May = 3, June–July = 14, August–September = 6, and October–November = 11. C) Monthly means (95% CI) of percent nitrogen content in vicuña pellets; samples sizes were late January = 14, mid-February = 7, late March = 13, late July = 5, early August = 10, and early November = 11. In B and C means with different superscripts were significantly different (Tukey test, $\alpha \leq 0.1$).

poor ($n_{\text{yearlings}} = 2, n_{\text{adults}} = 19, n_{\text{old adults}} = 5$) and good ($n_{\text{yearlings}} = 7, n_{\text{adults}} = 20, n_{\text{old adults}} = 4$) condition was similar among age classes ($\chi^2_2 = 2.49, P = 0.29$).

Forage and diet quality.—Percent nitrogen content in plants was higher (Mann–Whitney $U = 1,004, P < 0.001$) in

midsummer–early fall (median $[Q_1-Q_3] = 1.2\%$ $[0.7-1.8]$, $n = 26$) than midfall–early summer (0.6% $[0.4-0.7]$, $n = 30$). Likewise, percent nitrogen content in vicuña pellets differed significantly among months ($F_{5,54} = 12.9$, $P < 0.001$, $n = 60$) being ~ 1.5 times higher in midsummer–early fall than in midfall–early summer (Fig. 3C). Percent nitrogen content in pellets was similar during 2008 and 2009 (both years: $\bar{X} \pm SE = 1.5\% \pm 0.1\%$; $t_{38} = 0.37$, $P = 0.713$).

Vicuña density.—Density estimates were similar in 2008 and 2009. Density (95% CI) was 9.5 (4.6–19.5) individuals/km² in 2008 and 12.7 (6.8–23.8) individuals/km² in 2009.

DISCUSSION

Birth mass was a critical factor for vicuña calf survival in San Guillermo National Park. Individuals with higher birth masses had better chances of surviving. This effect was particularly strong during the 1st week of life, suggesting that there was a threshold for birth mass below which calves were likely nonviable. Birth mass in ungulates is partly dependent on the mother's body condition (Lomas and Bender 2007; Thorne et al. 1976; Verme 1965), which is ultimately influenced by females' access to high-quality food resources during pregnancy (reviewed by Gaillard et al. 2000). Vicuñas give birth at the onset of the growing season (Ruiz Blanco et al. 2011) and produce calves with birth masses $\sim 37\%$ larger than expected from the mother's body mass (Hofmann et al. 1983; Robbins and Robbins 1979; this study). Thus, vicuñas incur high energetic costs before new plant growth resumes. Most early mortality of low-birth-mass vicuñas occurred within 48 h after birth and resulted mainly from nonpredation factors. These observations suggest that food resources during pregnancy play a key role in early survival of vicuña calves.

High cohort birth mass in 2010 correlated with calves from that year surviving at a higher rate than those born in 2009. In ungulates, population density (Clutton-Brock et al. 1982; Sarno and Franklin 1999b) and environmental factors (Adams et al. 1995; Smith et al. 1997) affect the access of pregnant females to food resources and consequently influence cohort birth mass (Smith and Anderson 1998). In San Guillermo National Park, cohort birth mass was correlated neither to vicuña density nor diet quality in the previous year. Perhaps vicuña densities were not sufficiently high to constrain access to food resources or degrade range conditions. Alternatively, interannual variation in cohort birth mass could have resulted from pregnant females being exposed to varying availability of forage before parturition. In fact, primary productivity, at least in the plains, was lower in January 2008–January 2009 ($\bar{X} \pm SD = 152 \pm 108$ kg ha⁻¹ year⁻¹) than in January 2009–January 2010 (245 ± 109 kg ha⁻¹ year⁻¹, 2-tailed $t_{16} = 1.8$, $P = 0.09$ [E. Donadio et al., in litt.]). If forage biomass is indeed influencing birth mass, then precipitation at the onset of the growing season, before births occur, should be a strong predictor of calf survival. Further research is needed to evaluate this hypothesis.

Puma predation was the primary cause of vicuña calf mortality, a result expected for ungulates living sympatrically

with large predators (reviewed by Linnell et al. 1995). Similarly, pumas were the leading cause of guanaco calf mortality in Chile (Sarno et al. 1999). However, vicuña calf losses to pumas (49%) were substantially lower than those reported for guanaco calves (79%). For guanacos, high losses resulted primarily from pumas selectively preying on calves, a pattern attributed to pumas favoring small-size individuals (Bank et al. 2002; Franklin et al. 1999; Wilson 1984). One-year-old guanacos weighed 40–42 kg (Sarno and Franklin 1999a), whereas adult vicuñas weighed 38–40 kg (Franklin 2011). Thus, it is possible that selection by size is relaxed, and predation pressure on calves reduced, when pumas prey on vicuñas.

Puma predation accounted for 91% of the yearling and adult deaths recorded, but did not consistently remove vicuñas in good or poor body condition. Instead, body condition of vicuñas killed by pumas varied seasonally. Likely, pumas killed vicuñas in good and poor condition according to their availability, which in turn reflected seasonal changes in primary productivity and forage quality. Similarly, previous research showed that pumas did not select ungulates based on body condition (Hornocker 1970; Pierce et al. 2000).

In contrast, we observed some evidence that body condition predisposed vicuñas to puma predation. Fat content of vicuñas killed in the riskier meadows and canyons was lower than was the case for the safer open plains. This was especially evident in early spring–early summer, when nutritional stress appeared to be worst. Food deprivation, particularly at the end of the nongrowing season, could induce vicuñas near starvation to trade safety for access to food resources (Sinclair and Arcese 1995). Individuals displaying this behavior would simultaneously enhance their chance of survival by obtaining forage during a critical period and reduce that chance by increasing predation risk.

We documented for the 1st time, to our knowledge, survival rates of vicuña calves and causes, patterns, extent, and timing of calf and adult mortality. Our results highlighted the importance of puma predation and low birth mass as proximate causes of vicuña mortality. Forage quantity was correlated with birth mass, whereas seasonal changes in forage quality appeared to influence adult susceptibility to predation. The influence of forage, however, should be interpreted with caution because of the short-term nature of our research. Indeed, how environmental factors (e.g., early-summer precipitation) affect forage and ultimately vicuña mortality has yet to be determined.

RESUMEN

En ungulados Neotropicales, la relación entre la mortalidad específica por edades y sus causas ha sido poco estudiada. Entre enero de 2008–abril 2011, investigamos los patrones de mortalidad de crías (<1 año de edad) y adultos de vicuñas (*Vicugna vicugna*) en el Parque Nacional San Guillermo, ubicado en los Andes centrales de Argentina. En este trabajo analizamos la relación entre el peso al nacer, la fecha de nacimiento y el sexo de las crías con la probabilidad de supervivencia durante el primer año de vida; cuantificamos las causas de muerte en crías y adultos; y exploramos la relación entre la productividad primaria, calidad del forraje y calidad de

la dieta y el estado nutricional de las carcasas de vicuñas adultas. El peso al nacer fue un buen indicador de la supervivencia durante el primer año de vida: un incremento de 1-kg (~18%) en el peso al nacer resultó en una declinación del 54% en el riesgo de muerte. Adicionalmente, un bajo promedio del peso al nacer en un año estuvo asociado con una baja tasa de supervivencia durante ese año, pero no con la densidad poblacional ni calidad del forraje en el año previo. La depredación por puma (*Puma concolor*) explicó $\geq 49\%$ ($n = 93$) y 91% ($n = 89$) de la mortalidad en crías y adultos, respectivamente. La condición corporal de las vicuñas adultas cazadas por pumas varió estacionalmente. Este patrón estuvo asociado con cambios estacionales en la productividad primaria, la calidad del forraje y la calidad de la dieta en vicuñas. La influencia de factores ambientales (e.g., precipitación al inicio del verano) sobre el forraje y, en última instancia, la mortalidad todavía debe ser determinada.

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