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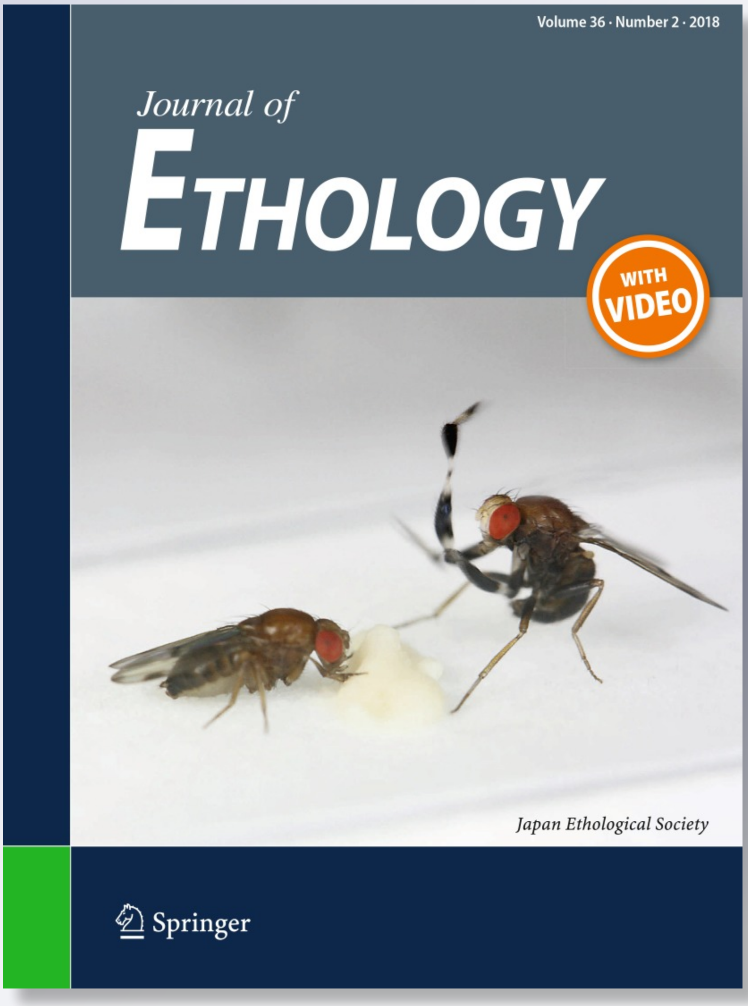

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ARTICLE

Social group dynamics and composition of managed wild vicuñas (*Vicugna vicugna vicugna*) in Jujuy, Argentina

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Abstract

The vicuña is a high Andean wild camelid that lives year-long in groups. We analyzed the social organization of 98 marked vicuñas after capture and live shearing, focusing on group composition, spatial patterns, territoriality and habitat use. The social units analyzed were families, bachelor groups and solo animals. Location fixes of 54 males and 36 females were registered over a 2-year period, and home range was estimated. All females belonged to family groups, and 8–12 month yearlings changed their home ranges prior to first reproduction at 2 years. Female yearlings dispersed to a new family group, while male yearlings dispersed to a bachelor group. Solitary males appeared during the interval between leaving bachelor or family groups, and vice versa. Our study showed that vicuña polygyny was based on female grazing area requirements. Females that stayed with the same males were defined as loyal, and had a mean 18.9 ha home range. Females that changed both to a different family and male; and grazed over the same home range size, were considered disloyal. Family groups selected the habitat that had a low stratum and the highest coverage of palatable plants, while bachelors used their habitat randomly.

Keywords *Vicugna vicugna* · Social groups · Territorially · Home range · Wildlife management

Introduction

The vicuña (*Vicugna vicugna*) is a wild camelid that lives in family groups throughout the year (Koford 1957; Franklin 1982). Research on the social behavior of the two subspecies of vicuña (*V.v. mensalis* and *V.v. vicuña*) shows that these populations are mostly sedentary and non-migratory, dividing into three social unit types: family groups, bachelor groups and solitary individuals (Koford 1957; Franklin 1974, 1982, 2011; Vilá 2000; Arzamendia and Vilá 2006, 2012). Some initial studies have described the mating system of vicuñas as a resource-defense type polygyny in which the territorial male defends an area of food resources essential to females (Franklin 1982, 1983, 2011). Other authors, such as Bosch and Svendsen (1987) and Vilá (1992), noted that territorial males herded females within their territories, thereby not allowing them to wander around. Therefore, the mating system also includes components of the harem defense system.

As mothers spend most of their time feeding or ruminating (Franklin 1982; Bosch and Svendsen 1987; Vilá and Cassini 1994), it is likely that the number of females grazing in their territory was the main resource that males gained from defending their area and periphery, from other males and predators. Living in groups has a direct effect on the reproductive success of the species as it allows females to graze unperturbed, increases the protection of calves from predators, and provides males with the opportunity to mate with all the adult females of the group (Vilá and Cassini 1994).

Although vicuñas are strong seasonal breeders, family groups nevertheless stay together throughout the year (Koford 1957; Franklin 1982, 2011). Mating and births occur from February to May (Franklin 2011; Arzamendia and Vilá 2012). The whole vicuña reproductive cycle occurs within the family group, including mating, birth and the weaning of calves.

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Males reach sexual maturity at 3–5 years of age, and a family group male will regulate group size by rejecting or accepting females, preventing resident females from leaving, and annually forcibly pushing out male young at 6–9 months, and female young at 10–11 months of age.

Young males will join male bachelor groups, while females eventually join another territorial male's family group (Franklin 2011). This pattern of year-long family groups is a rare type of social organization in mammals, exclusive to South American camelids (Koford 1957; Franklin 1974; Wilson 1980; Cassini et al. 2009). The mean family group size is that of 6 individuals—1 male, 3 females and 2 calves—and is common across different geographical areas, habitats, subspecies and environments (Franklin 1983; Glade and Catan 1987; Villalba 2000; Cajal and Bonaventura 1998; Borgnia et al. 2006; Arzamendia and Vilá 2012). Bachelor groups consist of bands numbering between 2 and 155 non-territorial males. The size of these groups fluctuates widely, and can even change in composition and size several times a day (Vilá 1995); 75% have less than 30 males, with 5–10 individuals being the most common group size (Franklin 2011; Arzamendia and Vilá 2012).

The vicuñas daily activity patterns and movements are also strongly influenced by the availability of water, especially during the dry season, given that they are obligated drinkers (Franklin 2011). Therefore, a family group's home range will encompass the area where the group is typically found grazing, and defended by the male. These ranges are encroached only by "passing vicuñas" which come to drink, given that drinking areas are not range-exclusive (Vila 1994).

The group dynamics of these animals have not been well studied, and in particular there has been no research concerning the social organization of managed, censused and marked animals (Franklin 2011). At our study site, the use of animal welfare techniques during capture and live-shearing resulted in no negative effects on the survival and birth rates of captured and uncaptured individuals (Arzamendia et al. 2010; Arzamendia and Vilá 2012). Furthermore, the group sizes—male, number of females and calves in the family groups—remained stable between pre- and post-capture censuses.

Our objective was to analyze social organization in wild marked vicuñas captured and, in some cases, shorn. To this end, we studied (1) group composition, (2) the spatial and temporal pattern of their distribution and territoriality, (home range) and (3) habitat selection and use.

Materials and methods

Study area

The present study was conducted in the Cieneguillas area, which is located in the Andean Altiplano within the Pozuelos Biosphere Reserve (66° 15′W, 21° 50′S) situated in Northwestern Argentina, at 3700 m asl. It has high diurnal temperature fluctuations and frequent frosts; rainfall is seasonal (December to March) and sparse (350 mm/year), and strong, dry winds are frequent. Phytogeographically it is part of the puna ecozone (Cabrera 1957). The study area comprises 8.9 km^2 and has one of the highest densities of vicuñas in Argentina (up to 40 vicuñas/km^2, mean 11.92 vicuñas/km^2) (Arzamendia and Vilá 2006). In some areas, vicuñas graze amongst livestock—llamas *Lama glama* and sheep *Ovis aries*) (Arzamendia and Vila 2015). The study area includes a capture field of 3.98 km^2.

This article forms part of the *Cieneguillas Wild Vicuñas Management Plan*, an initiative that ensures compliance with high animal welfare standards (Arzamendia et al. 2008). The capture and handling events of vicuñas were approved by the Provincial Directorate of Environment and Natural Resources of Jujuy, Argentina (DPMAyRN Permits Nos. 038-03, 130-04, and 203-05). Our procedures also complied with the guidelines set by the American Society of Mammalogists (Gannon and Sikes 2007).

In total, 98 vicuñas were captured and marked in 2003. An initial capture of 43 vicuñas, without shearing, was undertaken in May 2003. A second capture was carried out in November 2003; this time 75 vicuñas were shorn (55 of these were marked for the first time, and 20 were recaptures of marked animals). The traditional capture technique used—known as *chaku*—is described in detail elsewhere (Arzamendia and Vilá 2012), and basically consists of driving vicuña groups into a corral by people on foot. Adult males and females that had never been shorn before were captured and shorn. Young below 1 year of age where not shorn, and were later released together with the adults. The vicuñas were blindfolded prior to handling. Handling involved recording data on sex and age, the latter was estimated by dental eruption and wear (Yacobaccio 2006). The vicuñas were marked using a numbered necklace made of flexible plastic and a tag on their ear.

We registered these animals using two different survey scales, a broader one that took in the whole study area (8.9 km^2) and included census by vehicle; and a detailed record of the captured animals by foot and vehicle for up to 2 years after capture; this was undertaken during 14 observation periods occurring between May 2003 and February 2005 in the capture field (3.98 km^2). From the first day after their release, we observed the marked animals for 2 weeks on a daily basis, then for 1 week a month for 6 months thereafter, and afterwards for a week per season (Fall, Winter, Spring, and Summer). We identified marked individuals as occurring in one of three social units, defined groups (family and bachelors), and as solo animals. For each group, we registered the individual's role variously as family male, family female, calf or bachelor male. We defined a group as comprising at least two adult animals that appeared to be aware of each another and that moved together. The maximum distance between animals and their nearest conspecific in the group was set at 50 m.

We censused the vicuñas using a vehicle along 14 fixed-width line transects. We drove at a speed of 10 km/h and recorded animals within 500 m of the central line of the transect. Because our study area was an open steppe, a visibility of 500 m was easily achieved. In this broader scale survey, we were able to identify unmarked, marked, and shorn vicuñas, recording the following data: (1) type of social unit; (2) GPS location and distance from group of vicuñas to waypoint; (3) number and identification of each individual per group; (4) number of carcasses, which we removed.

Social composition and dynamics of marked vicuñas

We analyzed the temporal variation in the number of both marked females and calves per family group using generalized linear mixed models (GLMM). The response variable was the number of females plus calves per group, modeled with a Poisson error distribution and link log.

For the comparison between before and after capture, the data from 1999 to 2005 was used. Each observation consisted of a group sighting, without individual identification of the animals. The explanatory variable was a fixed factor with two levels, before and after the capture. An alternative model with one level for each year was also tested.

For the rest of the analyses, we used the data between May 2003 and February 2005, which included the identification of individuals and groups. Each observation was a sighting of a group during an observation period. The explanatory variables were included in these models as both fixed and random terms. The fixed terms tested were number of females at the first sighting of the group (defined by the criteria of male stability, measured in relation to the permanence of the females in the group—this was delimited as a factor with 3 levels, 1, 2 or more females), age of the male (continuous), and number of months of follow-up of the group. The random terms tested included the identity of the group as a random intercept to account for repeated measures (GROUP; 20 in total), and the observation month as a random slope (PERIOD; from 1 to 21). For all models, the goodness-of-fit was evaluated in terms of the Akaike information criterion (AIC) (Akaike 1974): the one that yielded the lowest AIC was preferred (Zuur et al. 2009). A maximum model was built including all variables, their interactions and quadratic terms. To check for co-linearity among variables, we calculated the variance inflation factors (VIFs) (Davis et al. 1986). Alternative models were generated using different combinations of random terms, also stepwise backward deletion of terms was performed to select significant terms to keep in the model. The terms were excluded from successive models if the AIC did not fall more than 2 points. Graphical verification of assumptions was performed (homoscedasticity and symmetry of residuals). All analyses were performed using the open-source software R 3.2.3 (R Core Team 2015).

We also analyzed family stability following the criteria of female stability in relation to permanence in the same grazing group with other females. To compare the frequency of males per type of group or social organization—family, bachelor groups and solitary individuals—we used the Fisher exact test (Crawley 2007).

Home range

The home range (HR) analysis comprised 54 males and 36 females, and entailed a mean of 11 location fixes per animal, with a minimum of 4 and a maximum of 26. Home range was calculated using the animal movement extension provided by the GIS software (Hooge and Eichenlaub 1997). Location fix coordinates were established using a global positioning system (Garmin Etrex), with an accuracy of 3 m radius. Data were processed using ArcView GIS (version 3.2a) in combination with the animal movement analysis ArcView extension (Hooge 1998). The results were projected on UTM 20S. A fixed kernel density estimation (Seaman and Powell 1996) was used to calculate home range. Animal movement analysis sets a fixed kernel with the smoothing factor calculated via least-squares cross-validation (LSCV), this is widely considered the most robust technique (Seaman and Powell 1996). Overlaps of core outlines around the given percentage of utilization density (kernel) were analyzed at 50% intervals. To visualize results obtained from overlap analysis, the arrangement of 50% kernel home range cores were projected on the study area map. Such home range cores can be considered centers of activity or exclusive home sites (Wronski 2005). To evaluate differences between the location of family and bachelor groups, the distance to the centroid of all observations was calculated with the aforementioned GIS program. We compared the size of 50% kernel home range cores between males and females, and between loyal females (those that were always with the same male) and disloyal females (those that changed males and group home range) using the Wilcoxon rank-sum test, with corrected rank-sum normal statistic (Crawley 2007).

Habitat use and selectivity

We assessed the vegetation units existing within the capture field in study area, thereby producing a vegetation map using GPS (Garmin Etrex) and the QGIS program. The habitats, or units, available within the study area were five—U1, U3, U4, U6, U12—of the fifteen units previously described by Arzamendia and Vilá (2006). The vegetation units were dominated by a high stratum of shrublands, or mixed shrub steppes and tussocks, with a low stratum of grasses and cushion plants. The total vegetation cover varied between 15 and 80%. Habitat quality was related to forage availability estimated as a mean percentage of vegetation cover for each vegetation category (vegetation community and stratum) (Arzamendia and Vilá 2015).

We measured habitat use and selection by evaluating the relationship between the use of a resource (unit vegetation), and its availability (area that it occupied) within the study area (Manly et al. 2002). We defined the complete home range as that generated by 95% of all locations of available habitats, and used the numbers of GPS locations for each group per habitat type (unit vegetation) in the studied period. Then we compared the group differences between family and bachelor groups in each habitat selection.

We undertook a log-likelihood chi-square test to determine whether the vicuña selectively used the habitats (Manly et al. 2002): $X^2 = 2\sum_{i=1}^{k}\left[n_{\mathrm{i}}^{0}\ln\left(n_{\mathrm{i}}^{0}/n_{\mathrm{i}}^{\mathrm{e}}\right)\right]$, where k was the number of habitat types, n_{i}^{0} was the quantity of habitat type i used by vicuña groups in the period, and $n_{\mathrm{i}}^{\mathrm{e}}$ was the expected quantity of habitat type i used. The null hypothesis was that vicuña groups used each habitat type in proportion to its relative abundance, i.e., they used each habitat type randomly. If the null hypothesis was rejected, then we would have to assume that at least one habitat experienced significant selection on the part of the vicuñas. We then determined which habitats within the home range were selected by applying the Manly–Chesson selectivity index and Bonferroni-adjusted 95% confidence intervals (Manly et al. 2002). A habitat type i was preferred if the lower confidence interval was > 1, and avoided when the upper confidence interval was < 1. If the interval included 1, then we assumed that the habitat type was randomly used (Manly et al. 2002).

Results

Social composition and dynamics of marked vicuñas

We captured and marked 98 vicuñas (41 females and 57 males) between May and November 2003. In May 2003, we captured 43 vicuñas belonging to 3 family groups (mean size: 1 male, 3 females, 1.33 calves) and one group of 27 bachelor males. In November 2003, we captured 75 individuals (55 were marked for the first time, and 20 were recaptured marked individuals). During the first month after release in November 2003, we found that 98% of the marked vicuñas had aggregated into 20 social units that also incorporated some unmarked animals. The twice-captured marked animals (adults and calves of three families and one bachelor group)—in May and November 2003—returned to their previous groups and territory (Table 1). The calves returned to familiar groups and were observed suckling. No calves were observed wandering on their own. The number of social units was usually constant, with a mean of 20 (DS = 1.97), although some individuals changed their social role within the population during the sampling period. Some marked bachelors ($n = 3$, 7.5%) dispersed to other areas during the reproductive period (February 2004), moving up to a distance of 20 km. We registered 7 dead marked vicuñas between May 2003 and November 2005.

All the females aggregated into family groups, excepting one yearling that was initially solitary, and joined a family group. Only the males changed from bachelors to family groups and vice versa; but same males also had solitary stints. (Table 2). We observed a mean of 1 male, 2.7 females (SE 0.07; min = 1, max = 7) and 1.46 calves (SE 0.11, $n = 28$) in the family groups with marked animals. We did not record any family groups with more than one adult male. No significant differences were observed by year, or before versus after capture, in the number of females or females plus calves for the 1999 to 2005 data (Table 3).

The best model for the number of females and calves observed during the 2003–2005 surveys included only the random term for the intercept identifying the group (AIC and residual deviance respectively: null model 489.6, 103.1; selected model 91.2, 87.2). The mean number of females predicted was 2.16 (mean = 0.7679 and SD = 0.2906 in the linear predictor scale). The observation period gave no additional information, indicating that the number of females did not change significantly during the survey and was mainly dependent on the group. There were no significant associations between the number of females of the groups and the age of the male, the initial number of females, or the number of months of follow-up. These results suggest that the number of females per group was not affected by the studied variables, and that it was stable for any given group during the survey.

Nearly half (47%) the marked males were family males (27 males), at least for a period of time; 40.77% of family males maintained their role. Some males from the bachelor group ($n = 2$) changed to a family role for a short period, and then returned to the bachelor group. Bachelor groups were 100% male, and constituted 2 groups, one large group that varied between 27 and 32 individuals and a smaller group of 3–4 males. The larger group tended to separate and fuse at different moments, while the smaller group was more stable. Solitary individuals were mostly males (91%) and one female (9%), maintaining this role between 1 and 3 months in total.

We observed 10 changes from bachelor males to family males. These changes occurred through different strategies: (a) by abducting a number of females from a family group ($n = 3$) after fights and other aggressions; and (b)

Table 1 Membership of marked individuals (M: male, F: female, and individual numbers, nm: non-marked, smn: shorn missing necklace) to different social groups (Bach: bachelor group, F: family group, soli: solitary)

Date		Social group and composition			
May 03	Nov 03	Males			
X	X	Bach 1	27 marked males		
	X	Bach 2	3 marked males		
	X	Soli	M9		
			Males	Females	Calves
	X	F	M14	F47, F80, Fnm	nm, nm, nm, nm
	X	F	M17	F11, F13, F102	M18, F45
	X	F	M38	Fnm, Fnm	F34
	X	F	M41	F6, F7	
	X	F	M42	F5	M43
	X	F	M48	Fnm	
X	X	F	M63	F67, F68, F175	
	X	F	M65	F91	F98
X	X	F	M70	F46, F151	F152, F153
	X	F	M72	F76	
	X	F	M73	F32, F71	F78, F79
X	X	F	M77	F75, F171, F173, F178	
	X	F	M92	F93, F94, F20	M118
	X	F	M95	F99	F96
	X	F	M157	Fnm	Nm
	X	F	Mnm	F74, Fnm	
	X	F	Msmn	F16, F97	
	X	F	Mnm	F69	
	X	F	Mnm	F50	Nm

First post-capture survey. Underlined: family males and loyal females throughout the study period (16–22 months)

Table 2 Changes in male social role

Initial status of male	Maintained	Changed	Total
Family	11	8	19
Solitary	1	8	9
Bachelor	23	16	39
Total	35	32	67

Table 3 Models for the number of females and females and calves per group

Model	D.F.	AIC females	AIC females and calves
Null	55	197.2	241.8
Factor year	51	202.7	246.1
Factor before/after the shearing	54	198.9	241.8

No factor was significant

by establishing a territory of their own ($n = 7$) and thereby attracting young females, including all marked female yearlings ($n = 6$), and some unmarked ones. The opposite, that of a family male becoming a bachelor, was registered 4 times. Two marked male calves joined the bachelors as yearlings.

In relation to social role stability, we found that solitary males showed the highest tendency towards changing their social role, while other social units were more stable (Fisher test $P = 0.035$, Table 2). Most of the changes in the groups occurred between December 2003 and April 2004, concurrent with the breeding season, and the yearling expulsion period (72% of changes recorded).

Each marked female was observed for a mean period of 13.26 ± 0.85 months (min. = 1 and max. = 16). Of the marked adult females, 45% gave birth during 2003, and this percentage increased to 65% in the following year. In the period between the 4th and 7th months post-release of both captures (May and November), we lost contact with one female (ID 44), and two others were registered as dead—F99 dead at a watering site, and F102 dead from unknown cause. We also found 3 dead calves—1 marked and 2 unmarked—presumably predated upon by a red fox (*Pseudalopex culpaeus*).

Although 35.5% of the total young and adult marked females stayed with the same male (loyal females), we observed that some females changed their males and families during the study period (disloyal females). Between November 2003 and February 2005, we observed a mean of 2.5 changes of family males (min = 1, max = 6) by the disloyal females. This data correlated positively to the length of time during which we recorded the marked females ($n = 31$; $r = 0.55$; $P = 0.0013$). We identified 15 female dyads or triads—inside the same group—that remained a mean of 10 months together (min. = 3; max. = 16).

The social pattern of distribution or territoriality

We analyzed the spatial distribution of the home range (HR) cores, an exclusive area that covered 50% of the home range. The arrangement of 50% kernel home range cores of young and adult males, as well as females were plotted on a map (Fig. 1). Such home range cores were considered to be centers of activity, or exclusive home sites. During the 16 months after the November 2003 capture, we gathered locational information on 26 females and 18 males. Two females and 7 males had fewer than 5 observations, and were therefore excluded from the HR analysis. The family group HR showed no significant differences between the sexes (females 19.92 ha, $n = 24$, min 6.25 and max 46.40 ha, vs males 13.92 ha, $n = 11$, min 12.46 and max 32.57 ha; $P = 0.072$) (Fig. 2).

The bachelor groups (Fig. 2, Table 1) were observed in the interspaces of adult family male cores, and around the periphery of the area. The mean distance between each location and the centroid of all observations was greater for bachelor groups (mean 822 m), than for family groups (mean 732 m, $P = 0.0021$). The monthly variation in this distance accounted for a full 33% of the total variation observed. Family males showed no simultaneous overlapping of their home range, while females changed area according to age and the accompanying male. Yearling females ($n = 6$) always changed their area and therefore males, at the time of their ejection from the group (Table 4).

Thirteen females (located 5 or more times) stayed with the same male (loyal females) (Table 1, Fig. 2), while the remaining females changed males 1–3 times (disloyal females). These two female strategies (being loyal or disloyal to the males), resulted in similar home ranges (18.858 ha, n = 13 vs 22.531 ha, $n = 7$ respectively; $P = 0.383$) acquired by remaining with a male that had a larger home range or by passing through areas with several males and then utilizing a combination of their smaller home ranges (mean size by male 6.15 ha). Loyalty was therefore associated with males that had larger home ranges (mean size HR 14.59 ha; Wilcoxon rank-sum test with rank-sum normal statistic with correction $Z = 1.9727$, P value = 0.0485).

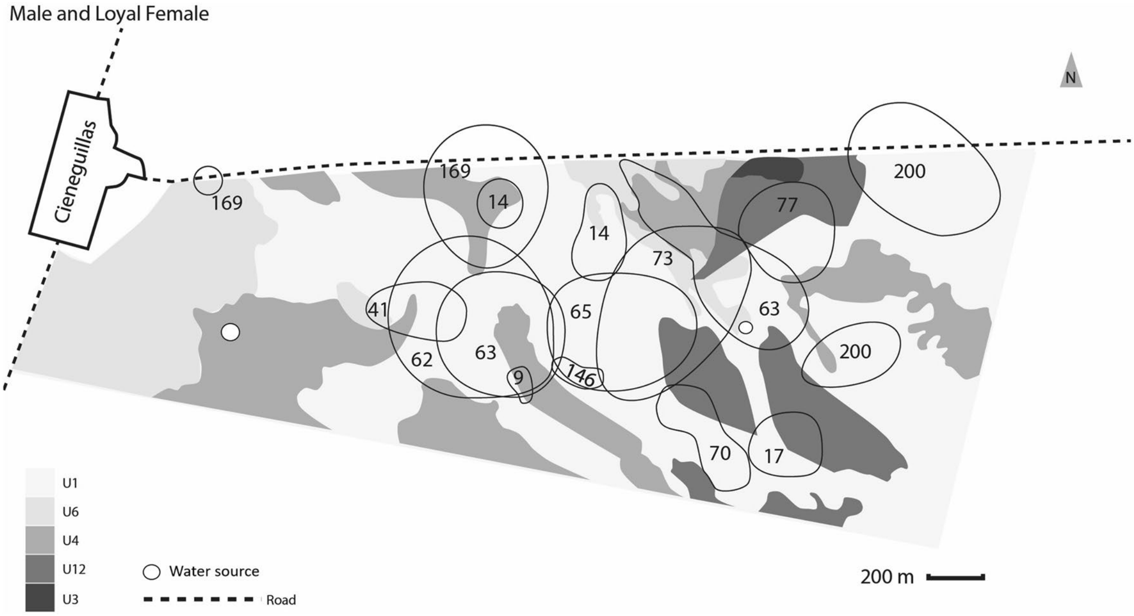

Fig. 1 Fifty percent home range cores of each male and their loyal females (see Table 1) (individualized by number of marked males), on habitat types of the study area. Family males did not overlap in their home range even when these intersected. References: (U1) shrub steppe of *Parastrephia quadrangularis* (tola) and tall grass *Jarava ichu*; (U3) tussocks dominated by tall grasses (*Festuca orthophylla*); (U4) shrub steppe of *P. quadrangularis* and *Tetraglochin cristatum;* (U6) "tolar"; (U12) shrub steppe of *T. cristatum*

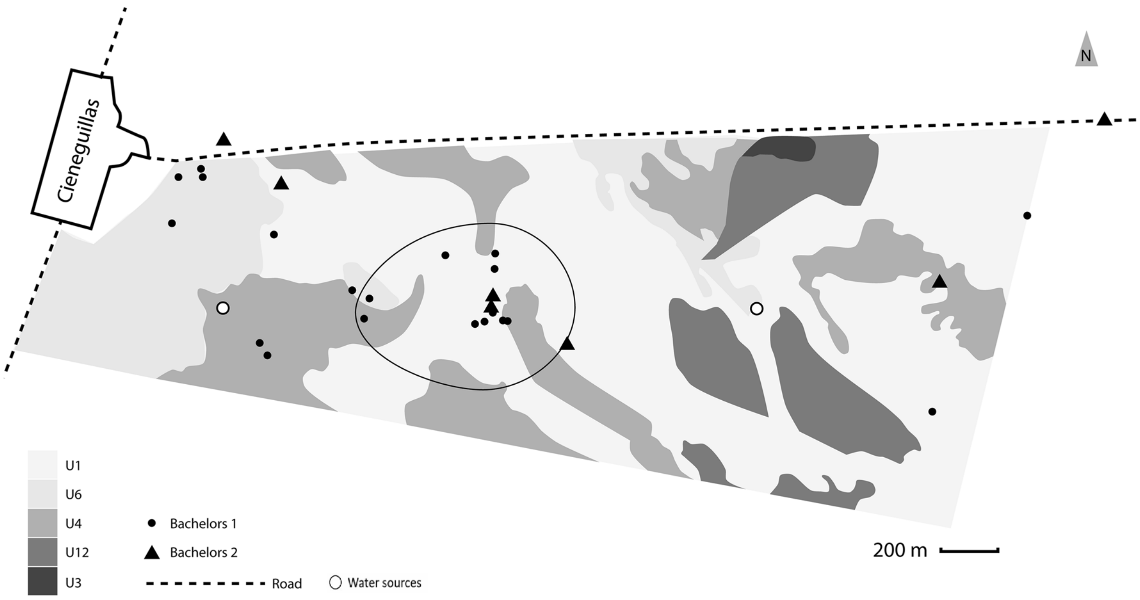

Fig. 2 Bachelor home range core and GPS locations (group 1), and GPS locations (group 2), and habitat types in the area and during period of study. References: (U1) shrub steppe of *Parastrephia quadrangularis* (tola) and tall grass *Jarava ichu*; (U3) tussocks dominated by tall grasses (*Festuca orthophylla*); (U4) shrub steppe of *P. quadrangularis* and *Tetraglochin cristatum*; (U6) "tolar"; (U12) shrub steppe of *T. cristatum*

Table 4 Movement of calf vicuñas between family male home ranges prior to first reproduction

ID Calf- sex	Born in HR male	Moved to HR male	Distance (m)
34 ♀	95	72, 169	1500–1600
45 ♀	17	137	880
78 ♀	73	147	673
96 ♀	95	146	553
110 ♂	Bachelors 2	Bachelors 2	–
118 ♂	63	death	–
152 ♀	70	137	708
153 ♀	70	169	1058

Habitat use and selection

Family groups were selective in the habitat type used ($X^2 = 121.4 > 20.52$; $P = 0.001$), while the bachelor groups observed in each habitat type were distributed proportionately to occurrence of habitat types ($X^2 = 6.65 < 9.49$; $P = 0.05$). Family groups selected the central zone that had the highest prevalence of grass cover in low stratum *P. quadrangularis* and *T. cristatum* (U4) shrub steppe, while the tolar (U6) and the mixed shrub and tussocks steppe of *P. quadrangularis* and Tall grass (U1) were underutilized. The other registered habitats were used according to their coverage (Table 5). There were two water sources which were always less than 1.5 km distant from individual vicuñas, and outside most of the core home ranges, which implied that vicuñas had to move to drink water.

Discussion

This is the first study where the behavior, social conformation and home range of marked vicuñas was systematically recorded. Capturing, marking and registering animals confirmed that the bachelor groups were composed of 100% males—some being sexually mature, while others were still non-reproductive. Capture and marking also showed that no family group had more than one male.

We recorded a mean family size (1 male, 2–3 females and 1–2 calves) similar to others recorded in previous studies (Koford 1957; Vilá 1992; Lucherini 1996; Franklin 2011; Arzamendia and Vilá 2012). Bachelor groups demonstrated synchronic behavior and varied in size, given that they tended to split into smaller groups or merge into larger ones (Koford 1957; Vilá 1995, 2000). The bachelor group sizes identified in our study were similar to those in other distribution areas (Koford 1957; Franklin 2011; Vilá and Roig 1992; Mosca Torres et al. 2015).

Our study registered the changing dynamics between bachelor groups, families and solitary individuals. Solitary animals were mostly males during the interval between leaving bachelor or family groups. Bachelor males changed to either solitary or family males. Some of the individuals belonging to these groups showed the greatest dispersal

Table 5 Vegetation units described by vegetal community; vegetation total mean cover (percentage TMC), area of vegetation unit, Manly–Chesson selectivity index (SI) and Bonferroni confidence limits (CL, L: low—U: upper) for family groups (FG) and bachelors (bach)

Habitat types or vegetation unit	Forage availability MC/stratum (%)	TMC (%)	Area (ha)	SI FG CL(L-U)	SI bach CL (L-U)
U1: Mixed shrub and tussock steppe of *Parastrephia quadrangularis* and tall grass (*Jarava ichu*.) (high stratum) and low stratum of grasses (*Bouteloua simplex* and *Cynodon* sp. grasses)	HS: 30–50 LS: 5	40–50	173.9	0.59 0.44–0.75*	0.88 0.62–1.14
U3: Tussocks dominated by tall grasses (*Festuca orthophylla*) and *P. quadrangularis*, with a low stratum of *Adesmia* sp., *Aristida antoniana,* and *Bouteloua simplex.*	HS: 28–35.5 LS: 15	40–50	1.4	1.17 − 0.66–3.01	0.00
U4 Shrub steppe of *P. quadrangularis* and *Tetraglochin cristatum*, with a low stratum of *Adesmia* sp., *B. simplex,* and *A. antoniana.*	HS: 20–30 LS: 20–40	30–60	60.9	2.76 2.56–2.97*	1.52 1.04–2.00
U6: Tolar, *P. quadrangularis* shrub and low stratum of (*B. simplex*, *A. antoniana,* and *Distichlis* sp.)	HS: 50–80 LS: < 5	50–80	58.2	0.24 − 0.22–0.70*	1.26 0.74–1.78
U12: Shrub steppe of *T. cristatum* with a low stratum of *A. antoniana* and *Adesmia* sp.	HS: 15–30 LS: 5–30	20–45	34.6	1.20 0.86–1.55	0.30 − 0.83–1.44
Total size study area (ha)			329		

*The proportions were estimated using a sample of 987 vicugna group observations in relation to the habitat type available area. $P < 0.05$ for Bonferroni confidence intervals α/2 K of the selectivity index. A negative lower limit for the confidence interval of 0% has been replaced by 0.00 since negative values for the selection indices are impossible. Confidence limits: lower > 1 is selection, upper < 1 is avoidance

distances. Bachelor groups included future breeding males, providing an essential genetic diversity reserve (Franklin 1982; Arzamendia and Vilá 2012). Changes in male social role were related to mating strategies. Male strategies included taking the place of a territorial male, and therefore its females; or alternatively defending an area that young females would then colonize. In our study, we found that female vicuñas needed a mean home range of roughly 18.9 ha, and that males were territorial; this is similar to the amount (18 ha) reported by Franklin (1983) in Pampa Galeras. These two interacting factors may explain the polygynous system of the species. Our results showed that females loyal to the same male over time had access to all of their home range, and that this tallied completely with a sole male's defended area (more than 18 ha), while the other disloyal females needed to use a similar area, but in conjunction with more than one male.

At our study site—an arid steppe zone—there were nearly homogeneous distributions of vegetation, so there were no clumped resources that could be monopolized by the family males at the family unit scale. Family groups selected the best type of habitats available, where the vegetation (U4) had a low stratum with the highest cover of palatable plants (*Bouteloua simplex, Aristida antoniana*, *Adesmia* sp.) (Borgnia et al. 2008, 2010). The tolar (U6) and mixed steppe (U1) where low strata had poor cover, was underutilized. Meanwhile, bachelor groups used habitats randomly in peripheral areas near villages or paths.

Our results imply that the defense of a territory with the best pastures is a cost for family males, but that defense of territories can increase their general fitness. Those males that defended large areas got permanent females (loyal), while those who defended only small areas had passing females (disloyal). Family groups occupying higher quality habitats have been previously reported (Arzamendia et al. 2006; Borgnia et al. 2010; Rojo et al. 2012; Arzamendia and Vilá 2015).

We observed that family core home ranges did not overlap, and that there was no association between different family adult males. This supported the hypothesis that males defended areas against other males to gain exclusive mating access to females. Taking into account the poor nutritional value of vegetation that often forces females to graze most of the day, it is interesting to note that males may be defending access for females to graze without harassment, thus increasing female fitness, and at the same time increasing their chances of obtaining and retaining females.

Among polygynous mammals, dispersal is usually male biased (Greenwood 1980), wherein males are responsible for gene flow, while females are predominantly philopatric (Wronski and Apio 2006). However, there is evidence to suggest that among a few mammalian species, female offspring disperse to avoid breeding with their father. This occurs when male tenure exceeds female age at maturity (Dechmann et al. 2007). Our results showed that the vicuña offspring from both sexes left their natal group before first reproduction, resulting in drastic changes to their home ranges, with the relocation of females to non-parental family groups, and males to bachelor groups.

In Koford's (1957) seminal work a mean of 7–12 changes in wild population (Aricoma, Peru) family groups during a 5-month observation period was reported. Similarly, as in Koford (1957), our most frequent change in family groups consisted of individual females moving between groups; this occurred between 1 and 7 times during the 14-month observation period. Our result was lower than Koford's so we inferred that capture did not affect these changes, and therefore had no noticeable effect on the social dynamics of the species in the area. Likewise, the birth rate of marked parents did not decrease in the year following capture. Further observation of unmarked and uncaptured groups can confirm this.

The regulation of group size can be viewed as the result of a game in which individuals distribute themselves between groups in such a way that they maximize their reproductive fitness (Sutherland 1996). The studied groups had a mean composition of between 2 and 3 females. This was previously identified as the optimal group size in terms of cost—more time alert/less time grazing—and benefits—number of females—per male (Vilá and Cassini 1994). In our study site, females attempted to have access to at least 18 hectares, so we considered that this strategy would lead to greater reproductive success.

We found two strategies in females: staying with a male with a large home range or changing between family groups to build their own home range. In this sense, the social organization of vicuñas is much more dynamic and interesting than has been previously reported. This non-dimorphic, "all-year-round" familial camel, is a unique model for studying ungulate behavioral ecology.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving humans This article does not contain any studies with human participants performed by any of the authors.

Research involving Animals All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study involving animals, such as the capture and handling of vicuñas, were in accordance with the ethical standards of the institution or practice at which the studies were conducted, and were approved by the Provincial Directorate of Environment and Natural Resources of Jujuy, Argentina (DPMAyRN permits Nº 038-03, 130-04, and 203-05). Our procedures also complied with the guidelines set by the American Society of Mammalogists (Gannon and Sikes 2007), the animal welfare protocols of GECS (South American Camelid Specialist Group), and the Species Survival Commission (SSC) of the IUCN, the International Union for Conservation of Nature.

Informed consent For this type of study formal consent is not required.

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