

THE VICUÑA

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Chapter 4

Sociality, Foraging and Habitat Use by Vicuña

Marcelo Cassini, Mariela Borgnia, Yanina Arzamendia, Verónica Benítez, and Bibiana Vilá

4.1 Introduction

In this chapter, we review the information on three aspects of vicuña (*Vicugna vicugna*) behaviour and ecology (1) intra-specific relationships, (2) foraging behaviour and ecology and (3) habitat utilization. We will also compare some of the behaviour and ecology of the vicuña with that of other South American camelid species, the wild guanaco *Lama guanicoe*, and the domestic llama *Llama glama* and alpaca *Lama pacos*. We will emphasize the spatial dimension of the vicuña's behaviour and the implications for the management of vicuña in protected areas.

4.2 Social Behaviour

We analyse three aspects of sociality of vicuñas (1) the social pattern of distribution or territoriality; (2) the differential distribution of sex and age categories between groups or group composition and (3) the distribution of individuals within groups.

4.2.1 Territorial Behaviour

Franklin (1974, 1982, 1983) conducted one of the first research projects on the social behaviour of vicuña; he concluded that they defend fixed group territories all year round. This study became a paradigm of animal behaviour studies, after being included as a main example in the famous book *Sociobiology* by E. O. Wilson (1980). The evolutionary argument was straightforward: In the extreme, harsh environment of the Puna desert, it was not enough for males to defend a territory only during the reproductive season to get access to females, but they must do it permanently. At the time when Wilson was writing his book, mating systems and social organizations were viewed as species-specific properties, so vicuña were seen as one of the clearest examples of a territorial mammal.

In studies that followed, it was assumed that vicuña defended permanent territories, but there were no systematic attempts to validate Franklin's result in other populations. The main difficulty was that laws prevented vicuña from being disturbed and captured and animals do not have pelage characteristics that can be used for individual identification. The only exception was the study conducted by Vilá (1994) who described the use of communal defecating sites (dung piles) by three well-known families, in Abrapampa (Argentina). She found some overlapping and tolerance between families that were found using the border areas and sharing the use of the peripheral dung piles (Vilá, 1994), in contrast to the fixed boundaries described by Franklin (1982). Similarly, a recent study at Cieneguillas (Argentina) (Arzamendia and Vilá unpublished data), for the first time, followed a large group of marked vicuña; they found that 19 harems and 1 bachelor group (a total of 98 vicuña) used specific portions of the landscape. However, there was overlap of harem areas, tolerance of neighbours, and the range of a harem was frequently used by another harem when the "owners" were absent. This suggests that territoriality is not as common as was initially postulated by Franklin.

4.2.2 Group Composition

Vicuña show three types of groups (1) family groups or harems, (2) bachelor groups and (3) solitary individuals. Harems are stable and permanent (all year round) while bachelor groups vary in size and can change in composition over a day (Vilá, 1995). In a comparative study, Vilá (2000) found that the mean harem size and composition was one male, three or four females and two calves, irrespective of environments, geographical areas, subspecies or seasons (Table 4.1).

There are some problems with the methodology used for determining harem composition – vicuña are not sexually dimorphic, so it is difficult to sex members

Table 4.1 Mean harem size of different populations (sites without country refer to Argentina)

Location	Mean harem size		Reference
	Females	Calves	
Ulla-ulla (Bolivia)	3.1	1.6	Cardozo (1981)
Pampa Galeras (Perú)	3.0	2.0	Franklin (1983)
Las Cuevas (Chile)	3.1	1.6	Glade and Cattán (1987)
Arequipa (Perú)	3.7	1.6	Davies 2003
Abrapampa (Argentina)	3.5	1.8	Vilá (1990)
Laguna Blanca (Argentina)	3.6	1.9	Vilá and Roig (1992)
Cieneguillas (Argentina)	3.4	2.0	Arzamendia and Vilá (2003)
Pozuelos (Argentina)	3.4	1.7	Renaudeau d'Arc and Vilá (1998)
Laguna Blanca Reserve (Argentina)	3.2	1.4	Borgnia et al. (2006a)
Olaroz Cauchari Reserve (Argentina)	3.9	1.8	Arzamendia et al. (2001)
Lagunas de Vilama (Argentina)	3.4	2.2	Arzamendia et al. (2001)

of groups in the field, and it is normally done using behavioural responses, which can produce uncontrolled errors. Even with the methodological limitations, several questions arise from this remarkably stable pattern of social organization:

- Why are harems not as large as bachelor groups?
- Why do females not breed alone or in pairs?
- Why do males remain in female groups outside the reproductive season?
- Why does group size not change between seasons or geographical areas?

Bonacic et al. (2002) found that female reproductive success, estimated as observed mean number of calves per female, decreased linearly with the number of females per group (Bonacic et al., 2002). Thus, from the point of view of the females, large groups represent a reproductive cost. Vilá and Cassini (1994) analysed the costs to males of group defence and they found a significant and substantial decrease in the foraging time of males when the number of females increased in their harems. In summary, there are advantages to both males and females in keeping family groups relatively small.

In the same way that there is evidence of costs to both males and females from living in large harems, we would expect to find costs associated with living in small ones. Arzamendia et al. (2006) found that solitary vicuña spent more time standing up (i.e. vigilant) and less time foraging than did members of groups (Fig. 4.1). They interpreted this result with the classical hypothesis within behavioural ecology that individuals can share vigilance behaviour within groups so that each individual spends less time scanning for predators, but that when added together groups are more vigilant than solitary individuals (reviewed by Krause and Ruxton, 2002). This means that individuals within groups are less likely to be predated upon and also have less time taken up with vigilance that could be put to other, more productive, behaviours.

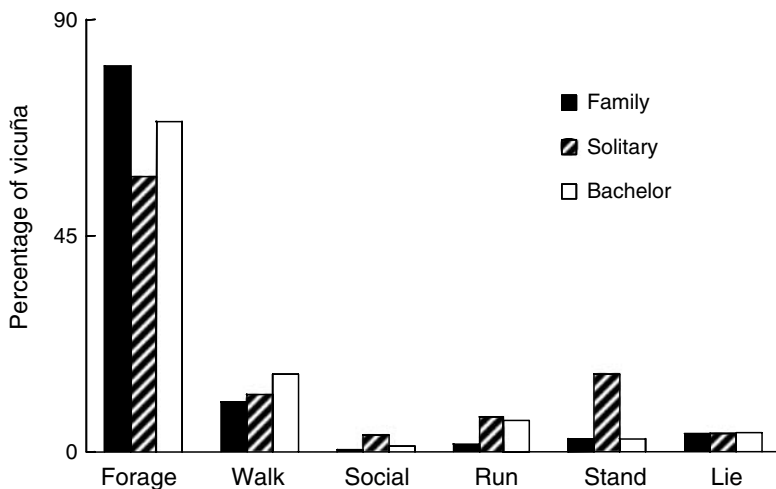


Fig. 4.1 Percentage of family and bachelor groups and solitary individuals of vicuña exhibiting different behaviours. Solitary vicuña spend more time standing (vigilant) and less time foraging than members of groups (from Arzamendia et al., 2006)

Another explanation for the lack of small groups in the wild is social constraints. In behavioural ecology theory, group size is viewed as the result of a “game” in which individuals distribute themselves between groups in a way that they maximise their reproductive fitness (Sutherland, 1996). There is a cost associated with intra-group competition for, for example, food and benefit from protection against predators, or selecting mates. A typical case is in foraging groups in which the cost of sharing food resources is compensated for by benefits of increased vigilance by the group. Under these conditions, it has been demonstrated that actual group sizes are generally larger than the predicted optimal group sizes, i.e., the sizes that maximize the benefit/cost balance (reviewed by Krause and Ruxton, 2002). In summary, the trade-off in social costs and benefits in small and large harems probably explains the size of harems and its constancy across areas and seasons.

Another enigma is why all female groups contain a male, and only one male, outside the reproductive season. The “harem” structure of winter groups clearly suggests that there is some kind of reproductive investment being made by males all year round. Franklin (1983) postulated that the extreme environmental conditions promote the defence of permanent territories by males; however, as previously discussed, territoriality does not appear to be a universal phenomenon for vicuña. So, rather than the defence of a patch of resources, family males probably contribute significantly to anti-predation vigilance and, more importantly, protect females from disturbance of vicuña of other groups, especially sexual harassment from bachelor males, even outside the breeding season. The role of male harassment avoidance in the evolution of breeding systems has been addressed for artiodactyls (Clutton-Brock et al., 1992, 1993) and other mammals (Cassini, 1999; Galimberti et al., 2000). In vicuña, harem holding males exhibit a strong intolerance for members of bachelor groups (Koford, 1957; Franklin, 1974; Vilá, 1995) which represent to constant source of disturbance for females within family groups.

The formation of year-round harems is a rare social organisation in mammals, however it is not exclusive to vicuña; guanaco males may also stay with female groups during the winter (although the social structure of this species is more plastic than that of vicuña, Franklin, 1982) suggesting that this behaviour is an ancestral social strategy of South American camelids.

4.2.3 Individual Distances

The spatial relationships and interaction between individuals are two important factors in describing social organization of wild mammals. Space maintenance had different interpretations of its selective advantages, including minimization of disturbance while feeding, reduction of interference while fleeing from danger and avoidance of transmission of infectious diseases (Wilson, 1980).

The distance between individuals has been traditionally used in sociobiology as a measured of the degree of social tolerance (Wilson, 1980). Individual distances within groups varied substantially depending on group types and the sex and age of

group members. The mean individual distance in bachelor groups (1.7 m) was smaller than between females in family groups (2.6 m) (Vilá, 1995). Harem holding males were peripheral to this group of females and the distance between the harem holding male and the closest females varied from 6 m while grazing and lying and a much greater when the male was involved in defence activities. The mean distance between a calf and its mother was related to age of the calf and occurred together with a reduction in the duration and frequency of suckling (Vilá and Roig, 1992) as predicted by the theory of parent–offspring conflict (Trivers, 1985). In family groups with more than one calf, calves tended to form “clubs” in which members played, stood and grazed together. Calves in clubs stayed further apart from their mothers than did solitary calves (Vilá, 1995).

4.3 Foraging Behaviour

Foraging behaviour is divided into four components: search for, selection of, ingestion of and digestion of food. While in carnivores, searching for food (including capturing it) is normally the most consuming component of foraging behaviour, in herbivorous mammals, the low quality of food means that ingestion and digestion requires more time than searching and selection of food (Stephens and Krebs, 1986). In this section, we describe the foraging behaviour of vicuña and other South American camelids, because some of the underlying mechanisms of foraging spatial decisions emerge from these inter-specific comparisons. Recent molecular studies of the taxonomy of South American camelids indicate that the alpaca is a domesticated form of the vicuña, while the llama derived from the guanaco (Kadwell et al., 2001); therefore, it is expected that vicuñas share more behavioural and physiological traits with alpacas than they do with llamas or guanaco.

4.3.1 *Activity Budgets and Overall Foraging Time*

Vicuñas vary the proportion of time invested in foraging depending on climatic conditions; Lucherini (1996) found that vicuña in Laguna Verde (Catamarca, Argentina) spent 69% of diurnal period foraging in summer, and in the same season, Vilá and Cassini (1993) obtained a similar value (71%) for a population in Abrapampa (Jujuy, Argentina). In the latter study, vicuña significantly increased foraging time in autumn, the beginning of the dry and cold season. In Laguna Blanca (Catamarca, Argentina) 78% of vicuñas were observed foraging at the end of dry season (Renaudeau d’ Arc et al., 2000). Mènard (1982) estimated this proportion in 89% for a population from Pampas Galeras (Perú) in a dry year, after several years of drought. Arzamendia and Vilá (2003, 2006) and Arzamendia et al. (2006) obtained a typical annual mean figure of 70% of the time foraging in Laguna Pozuelos (Jujuy, Argentina). This adjustment of foraging time to climatic conditions

likely to result from the digestive capabilities of camelids as, in the dry season, they need to ingest more low-quality grasses meet their need for energy and nutrients.

In a comparison of behaviour between the sexes, it was found that adult females spent more time foraging than did adult males (Vilá and Cassini, 1994; Arzamendia and Vilá, 2003; Arzamendia et al., 2006), probably because of the costs of gestation and lactation which increase both nutritive and energetic demands on emales.

Although they had a similar total grazing time, the time that individuals spent at a feeding station (i.e. an area that a foraging animal can reach without moving its feet) is longer in llamas than alpacas but bite rate is greater in alpacas than in llamas (Pfister et al., 1989). Guanaco spent more time foraging than did vicuña (Lucherini, 1996) probably because of differences in body size, with llamas and guanaco requiring a greater absolute amount of food than alpacas and vicuña. All camelids had larger foraging time than did sheep have (Pfister et al., 1989), most likely due to the digestive differences between groups of Artiodactyls (see later).

4.3.2 Food Searching and Daily and Seasonal Movements

The movements of the herbivores in their search for food follow a route that can be described as a daily spatial pattern of activity. In vicuña, daily movements from sleeping areas on the mountain slopes to foraging and drinking areas on the plains have been described (Franklin, 1974; Vilá and Roig, 1992). This pattern was not observed in areas where water sources are abundant suggesting that daily movements are governed by the vicuña's daily need for drinking water (Franklin, 1983). In pioneering work, Koford (1957) said that vicuñas were never found more than a mile away from water.

Vilá and Cassini (1993) found a change in the daily rhythm of activity over the year: in the warm/wet season there was a peak of resting and standing at noon that disappeared in the cold/dry season.

Recently, Laker and Mundsén (personal communication) have postulated the occurrence of seasonal movements or of annual migrations of vicuña in response to seasonal changes of food availability at a landscape scale.

4.3.3 Botanical Composition of Diets and Diet Selection

There are few studies of the diet of vicuña; traditionally vicuña have been described as grass feeders (Koford, 1957; Franklin, 1982; Mènard, 1984), mainly adapted for grazing on forbs and perennial grasses close to the ground. They are the only Artiodactyls with open-rooted, continuously growing incisors. In Pampa Galeras, Franklin found that vicuña avoided some tall coarse bunch grass such as *Festuca dolichophylla* and *Stipa* spp. but preferred other more nutritious plants such as *Festuca rigesens* and *Deyeuxia vicugnarum*. Aguilar et al. (1995) described an annual pattern of diet

selection in Abrapampa (Jujuy, Argentina), where in the dry season (winter) vicuña consumed mainly *Festuca scirpifolia*, a tall grass with low quality but high biomass. In the wet season (summer), vicuña preferred short grasses as *Deyeuxia nardifolia*, *Hordeum andicola*, *Distichlis humilis*, *Carex* spp. and *Eleocharis* spp. Cajal (1989) studied the diet of vicuña and guanaco in San Guillermo Reserve (San Juan, Argentina). There, the diet of both species was similar but guanaco ate more tall grasses, while vicuña fed on forbs and short grasses more intensively. Cajal's study area included some shrub steppes, and vicuña were also found to browse on them to a limited extent. Foraging on shrubs was also found in Laguna Blanca Reserve (Catamarca, Argentina) (Benítez et al., 2006) and in Laguna Pozuelos (Jujuy, Argentina) (Arzamendia, unpublished data). The genera of shrubs preferentially consumed by vicuña are *Adesmia*, *Verbena*, *Acantholippia* and *Tetraglochin* spp.

During the wet season in Laguna Pozuelos, vicuñas were more likely to use the low gramineous-herbaceous stratum, with high nutritional value (FIDA, 1991) and/or high biomass annual grasses like *Bouteloua simplex*, *Aristida* spp., *Adesmia* spp. and *Eragrostis curvula*. In the dry season, they were more likely to use the vegetation units with high cover of grass and shrubs in both strata (Arzamendia and Vilá, 2006).

The differences found between vicuña and guanaco were similar to those found between their domestic relatives, alpacas and llamas. Several studies have been conducted on the diet of llamas, alpacas and sheep in the Peruvian Puna. Although the results are variable, the overall trend is that alpacas have a diet that is intermediate in competition between llamas and sheep; llamas select for tall, coarse bunch grasses, while sheep consume short grasses and forbs (San Martín and Bryant, 1989; Pfister et al., 1989). Alpacas appear to have the most catholic foraging behaviour, depending on the condition of vegetation; in the wet season, they use tall grasses as llamas do, while in dry season they move to feed on short grasses, forbs and sedges (Reiner and Bryant, 1986).

In summary, vicuñas forage mainly on poaceae and ciperaceae, adding variable proportions of shrubs to their diet in steppes habitats. Vicuñas and alpacas show similar food preferences, and have a diet that is intermediate between llamas (and guanaco) and sheep.

4.3.4 Intake Rate and Digestive Capabilities

Recently, Van Saun (2006) reviewed the nutrient requirements of domestic South American camelids; there are several studies on ingestion and digestion of llamas and alpacas, but none on vicuña. These studies indicated that camelids showed several morphological and physiological differences to the other ruminants of the order Artiodactyla (Jouany, 2000), that appear to be adaptations to consuming coarse forage where nutrients are diluted by structural carbohydrates which are difficult to digest (San Martín and Bryant, 1989). The feed intake in alpacas was clearly related to forage quality, being negatively correlated with lignin content of forages and positively correlated with their digestibility (Lopez et al., 1998).

As expected, South American camelids have higher digestive efficiencies than goats (*Capra hircus*) when fed on C4 grass hay, but not on C3 grass hay (Sponheimer et al., 2003). C4 grasses tend to have lower nitrogen and higher cell wall concentrations than their C3 counterparts, and they concentrate protein in highly vascularised bundle sheath cells, which are more difficult to digest (review by Sponheimer et al., 2003). South American camelids have a high capacity to digest hemicellulose, which is very important under natural conditions, since they are very selective for grasses which contain high levels of hemicellulose (Lopez et al., 1998).

The ability of camelids to digest fibrous forages has been attributed to several mechanisms (review by Lopez et al., 1998) (1) efficient nitrogen recycling due to a low renal excretion, and a high ruminal retention time for the solid phase, which favours cell wall degradation via a longer exposure time to microorganisms; (2) the pH of the rumen contents, which is close to neutral favouring cellulolytic digestion; this is due to bicarbonate secretion in the first two stomachs of the rumen and (3) high concentrations of volatile fatty acids in the first two stomachs, which could be explained by the high pH that neutralised these acids, keeping them as ions which are more slowly absorbed, therefore they can be used as an energy source.

Although llamas and alpacas are generally considered to have identical nutritional requirements when corrected for body size (e.g. San Martín and Bryant, 1989), Sponheimer et al. (2003) demonstrated that llamas have much higher digestible dry matter intake relative to metabolic weight, suggesting that llamas perform better on low-quality forages than do alpacas (Sponheimer et al., 2003).

In summary, camelids show physiological adaptations to foraging on the vegetation of dry environments, especially grasses. However, alpacas and vicuñas perform worse than llamas and guanaco, and so depend more on selecting high quality grasses and forbs.

4.4 Habitat Use

One of the key aspects of vicuña ecology is habitat use because it is well known that vicuñas use only a small proportion of their potential habitat in protected areas. This phenomenon was originally recognized in a seminal paper by Koford (1957), and subsequently described in several studies conducted in different protected areas of the vicuña's geographical range (Cajal, 1989; Franklin, 1983; Renandeu d'Arc et al., 2000; Arzamendia and Vilá, 2003, 2006).

The Puna region is characterized by three types of landscapes: the typical elevated plain that defines the region ("altiplano" or "puna"); the peaks and pronounced slopes of the mountains; and the intermediate fringe of smooth slopes ("piedemonte"). Vicuña used both the piedemonte and the plain.

The most common habitats types in the Puna are (1) xerophytic shrub steppes frequently mixed with short grasses and forbs; (2) bunchgrasses steepes; (3) open rocky areas with sparse vegetation; and (4) wetlands of short plants with high ground cover ("vegas" or "bofedales"). Several studies analysed the use of these types of habitats; in Pampas Galeras (Perú) vicuña preferred foraging on three

vegetation types: two grassed steppes dominated by *Festuca rigesens*, *Calamagrostis vicunarum*; and the vegas (Franklin, 1983). In the Ulla-Ulla (Bolivia), two main habitats are found: grass steppe and vegas, and vicuña preferred vegas, although the availability of this habitat depended on the presence of people and alpacas (Villalba, 2003). In the San Guillermo Reserve (Argentina) three main habitats are found (1) plains with tussock grassland; (2) gentle, grassy slopes and (3) rocky slopes (Cajal, 1989); vicuñas were more abundant in the grassland plain and there was a positive correlation between vicuña density and plant cover. In the Laguna Pozuelos (Argentina) vicuña also preferred vegetation communities dominated by grasses (“pajonal” and “esporal”), with high plant cover (located in plains and “piedemonte”) and were less frequently observed than expected in habitats with low vegetation cover dominated by shrubs (located in the peaks and pronounced slopes of the mountains) (Arzamendia et al., 2006). In the Laguna Blanca (Argentina), vicuña avoided the open rocky areas and the areas dominated by the shrub *Acantholippia hastulata* (Renandeu d’Arc et al., 2000). A more recent study in the same reserve, analysing a larger area, indicated that grass and mixed steppes were also intensively used by vicuña (Borgnia et al., unpublished data).

This pattern of habitat selection with preferences for certain grassland steppes and vegas is consistent with results on diet composition, that found that vicuña forage mainly on poaceae and ciperaceae (Koford, 1957; Franklin, 1983; Cajal, 1989; FIDA, 1991; Aguilar et al., 1999; Borgnia et al., unpublished data).

Arzamendia et al. (2006) described a change in habitat selectivity between years in Laguna Pozuelos (Argentina) (Fig. 4.2); they found that, in 2002, availability of

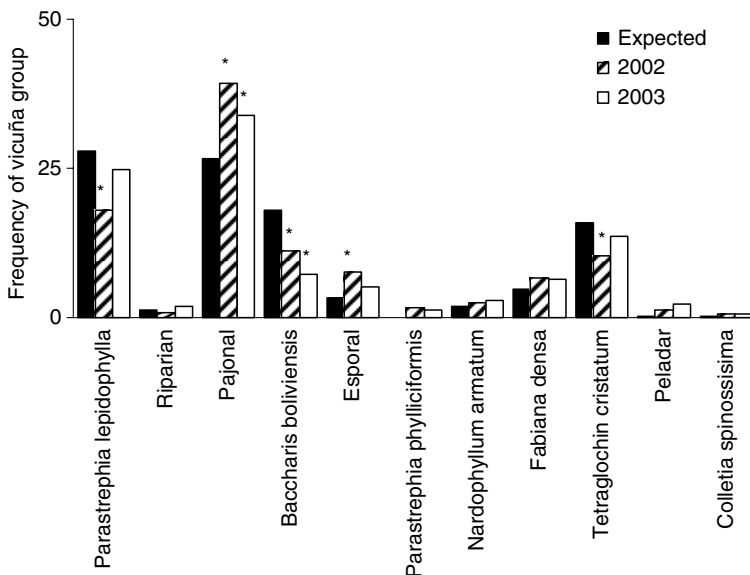


Fig. 4.2 Number of groups of vicuña in different habitats, expected for the area occupied by each habitat type, and observed in 2002 and 2003. In 2002, vicuña preferred or rejected five habitats, while in 2003, only two, suggesting a decrease in selectivity between years (from Arzamendia et al., 2006)

vegetation (grossly estimated from plant cover) was higher than in 2003 (a dry year) for all habitat types. Habitat selection theory predicts that when resources are concentrated in good habitats, most individuals will use these habitats; however, when the availability of resources decreases in good habitats, the less competitive individuals will move to low-quality habitats (Sutherland, 1996). The result is a more homogeneous distribution between habitats, as it was observed in Pozuelos. This phenomenon is called “buffer effect”, and its intensity depends on the nature of intra-specific competition (Gill et al., 2001). Bonacic et al. (2002) recognized the role of competition in the population ecology of vicuña. They found evidence of density dependence in vicuña populations and suggest that long-term density-dependent relationships are modulated by between-year changes in precipitation and food availability. The buffer effect is a possible spatial mechanism that mediates density-dependency in vicuña.

There is evidence of a negative relationship between the distribution of domestic ungulates and vicuña (Arzamendia and Vilá, 2003; Villalba, 2003). For example, Borgnia et al. (2006b) found a significant negative correlation between the distribution of vicuña and domestic species (including cattle, donkeys, sheep and goats, and llamas) in a 2-year study conducted in Laguna Blanca (Argentina) (Fig. 4.3). Domestic species are normally taken to vegas for grazing, and vicuñas avoid using the vegas when domestic species are present. There is no evidence of direct competition, and vicuña and domestic species can be observed foraging in the same areas without displacements or agonistic interactions. However, vicuñas are disturbed by the presence of people and dogs, which is probably one reason for vicuña’s avoidance of vegas when domestic species are present (Arzamendia and Vilá, 2003; Villalba, 2003). Overgrazing of vegas is common in the Puna (Braun

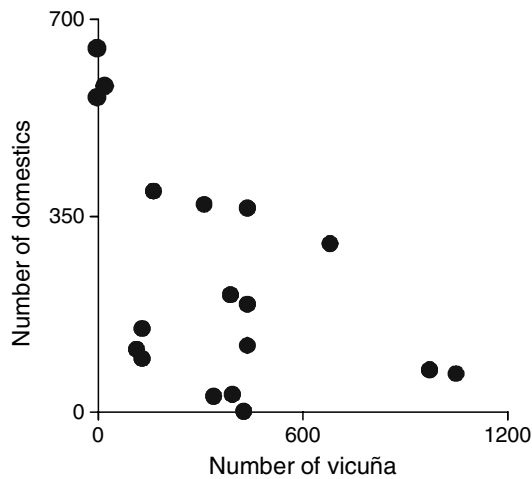


Fig. 4.3 Negative correlation between the distribution of vicuña and domestic ungulates ($r = -0.53$, $p < 0.05$) (from Borgnia et al., 2006b)

Wilke et al., 1999; Céspedes et al., 2003; Alzerreca et al., 2003; Bautista et al., 2003), so the use of vegas by domestic species can also substantially reduce the biomass of vegetation available for vicuña, and could be an explanation for vicuña's avoidance. Finally, the ability of camelids to use low quality grasses (as described previously) can make them less dependent on vegas than are sheep and cattle, and can explain the spatial segregation without the occurrence of competition or interference. Future work is required to discriminate between these hypotheses.

Few studies have investigated the spatial relationship between vicuña and the other wild camelid, the guanaco. In the Laguna Verde (Catamarca, Argentina) Lucherini and colleagues (Lucherini, 1996; Lucherini and Birochio, 1997; Lucherini et al., 2000) found a degree of altitudinal segregation between the species and a higher frequency of guanaco in close proximity to water than vicuña. In the San Guillermo Reserve (San Juan, Argentina), Cajal (1989) found differences in habitat use by family groups and solitary males of both species.

In a recent study conducted in Laguna Pozuelos, Arzamendia and Vilá (2006) found differential use of habitat between types of groups of vicuña. Family groups were mainly associated with piedemote and paleolacoon (with smooth slopes and major vegetation cover), while bachelor groups use mainly mountains (with high slopes and low vegetation cover).

4.5 Final Comments, Including Relevance to Conservation

We described the behaviour of vicuña, without offering an extensive description of forms and functions. For example, we present new evidence that challenges the “myth of permanent territorialism” and propose a plastic spatial organization, with habitat selection and daily movements adjusted to the huge changes in resource availability in the Puna desert. Another example is the importance of digestive physiology as a foraging constraint that determines the range of food types consumed and consequently governs habitat selection in different seasons. A third example is the new evidence of spatial segregation between vicuña and other wild and domestic ungulates.

There are still several traits of vicuña behaviour that require further study. It is of fundamental importance to conduct research on a population of marked individuals that offers a more definitive explanation of the social organization of this species. A study that simultaneously analyses population distribution at habitat and landscape level, food availability and quality, and diet, both of vicuña and domestic species, is also urgently required.

Most vicuña populations are now classified under Appendix II of the Convention International for Trade on Endangered Species (CITES); as a consequence, many projects of exploitation of vicuña for their fibre have been initiated in the Andes, and there is a strong pressure on local authorities and communities to expand the commercial use of this species (Lichteinstein and Vilá, 2003). Most of the research conducted at present is technically orientated and has the practical objective to

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There are still several traits of vicuña behaviour that require further study. It is of fundamental importance to conduct research on a population of marked individuals that offers a more definitive explanation of the social organization of this species. A study that simultaneously analyses population distribution at habitat and landscape level, food availability and quality, and diet, both of vicuña and domestic species, is also urgently required.

Most vicuña populations are now classified under Appendix II of the Convention International for Trade on Endangered Species (CITES); as a consequence, many projects of exploitation of vicuña for their fibre have been initiated in the Andes, and there is a strong pressure on local authorities and communities to expand the commercial use of this species (Lichteinstein and Vilá, 2003). Most of the research conducted at present is technically orientated and has the practical objective to

improve vicuña exploitation. However, effective sustainability in the long term can only be achieved with deep knowledge on vicuña ecology. Therefore, studies on key aspects of the ecology of vicuña are urgently required to evaluate and if possible to minimise the impact and guarantee environmental sustainability of the use.

References

- Aguilar MG, Martin GO, Neumann R, Chagra Dib EP (1995) Estimación de la composición botánica en la dieta de la vicuña (*Vicugna vicugna*) en la puna jujeña. *Revista Argentina de Producción Animal* 15:343–346.
- Aguilar MG, Chagra Dib EP, Neumann R (1999) Rangeland in the diet of vicuñas. *Progress in South American Camelids Research* 105:329–333.
- Alzerreca H, Prieto G, Laura J (2003) Utilización de forraje de los bofedales y gramadales en el altiplano y altoandino de Bolivia. In: CIF, FCAyP-UMSS (eds), *Memorias del III Congreso Mundial sobre Camélidos*, 1er. Taller internacional de DECAMA, Vol I., Potosí, Bolivia, pp. 415–421.
- Arzamendia Y, Vilá B and Tecchi RA. (2001) Las poblaciones de vicuña (*Vicugna vicugna*) en la Reserva Laguna de Pozuelos y otras áreas de Jujuy. V Congreso Latinoamericano de Ecología. San Salvador de Jujuy, Argentina.
- Arzamendia Y, Vilá B (2003) Estudios de comportamiento social de vicuñas en la RB Laguna de Pozuelos, Jujuy, Argentina, como línea de base para el manejo sostenible de la especie. In: Cif FC (ed), *Memorias del III Congreso Mundial sobre Camélidos*, 1er. Taller internacional de DECAMA, Vol I., Potosí, Bolivia, pp. 187–192.
- Arzamendia Y, Vilá BL (2006) Estudios etoecológicos de vicuñas en el marco de un plan de manejo sustentable: Cieneguillas, jujuy. In: Vilá B (ed), *Investigacion, conservacion y manejo de la vicuna*. Proyecto MACS, Talleres Graficos Leograf, Valentin Alsina, Argentina, pp. 69–83.
- Arzamendia Y, Cassini MH, Vilá BL (2006) Habitat use by vicuñas, *Vicugna vicugna*, in Laguna Pozuelos Reserve (Jujuy, Argentina). *Oryx* 40:1–6
- Bautista J, Escalier G, Mamani P, Copa S, Marin W (2003) Productividad de bofedales según carga animal para dos épocas en Ulla Ulla. In: CIF, FCAyP-UMSS (eds), *Memorias del III Congreso Mundial sobre Camélidos*, 1er. Taller internacional de DECAMA, Vol I., Potosí, Bolivia, pp. 457–460.
- Benítez V, Borgnia M, Cassini MH (2006) Ecología nutricional de la vicuña (*Vicugna vicugna*): un caso de estudio en la Reserva Laguna Blanca, Catamarca. Chap. 5, In: Vilá B (ed), *Investigacion, conservacion y manejo de la vicuna*. Proyecto MACS, Talleres Graficos Leograf, Valentin Alsina, Argentina, pp. 51–67.
- Bonacic C, McDonald DW, Galaz J, Sibly RM (2002) Density dependence in the camelid *Vicugna vicugna*: the recovery of a protected population in Chile. *Oryx* 36:118–125
- Borgnia M, Vilá BL, Cassini MH (2006a) Estimación poblacional local y estructura social de vicuñas en la Reserva Laguna Blanca, Catamarca. *Proceedings del IV Congreso Mundial sobre camélidos*. Eje Ecología, Conservación y Manejo. Santa María, Catamarca (Argentina) pp. 11–15.
- Borgnia M, Vilá BL, Cassini MH (2006b) Distribución y uso de hábitat de la vicuña en una zona de la puna catamarqueña con actividad pastoril. XXII Reunión Argentina de Ecología. Córdoba (Argentina), Asociación Argentina de Ecología, Córdoba, Argentina.
- Braun Wilke RH, Pichetti LPE, Villafañe BS (1999) *Pasturas montanas de Jujuy*. Facultad de Ciencia. Agrarias. Universidad Nacional de Jujuy, Argentina.
- Cajal JL (1989) Uso de hábitat por vicuñas y guanacos en la Reserva de Biósfera San Guillermo. *Vida Silvestre Neotropical* 2:21–31

- Cardozo A (1981) Evolución poblacional de vicuñas en Ulla Ulla, Bolivia, 1965–1981. Estudios especializados, EE-25. INFOL, La Paz, Bolivia.
- Cassini MH, (1999) The evolution of reproductive systems of pinnipeds. *Behavioral Ecology* 10:612–616.
- Céspedes J, Alzerreca H, Prieto G, Laura J (2003) Intercambio ingreso/carga animal en bofedales de Ulla Ulla. I. In: CIF, FCAyP-UMSS (eds), *Memorias del III Congreso Mundial sobre Camélidos*, 1er. Taller internacioal de DECAMA, Vol I., Potosí, Bolivia, pp. 461–466.
- Clutton-Brock TH, Price O, MacColl A (1992) Mate retention, harassment and the evolution of ungulate leks. *Behavioral Ecology* 3:234–242.
- Clutton-Brock TH, Deutsch JC, Nefdt RJC (1993) The evolution of ungulate leks. *Animal Behaviour* 46:1121–1138.
- Davies J (2003) Population ecology of the vicuña (*Vicugna vicugna*) at the Salinas y Aguada Blanca National Reserve, Arequipa, Perú: baseline data for sustainable management. Masters Thesis. University of Florida.
- FIDA (eds) (1991) Programa Regional de apoyo al desarrollo de la crianza de camélidos sudamericanos (Argentina, Bolivia, Chile, Ecuador y Perú): la crianza de camélidos y características de la producción. Annex. IV, Report 0334. Fondo Internacional de desarrollo agrícola (FIDA).
- Franklin WL (1974) The social behaviour of the vicuña. In: Geist V, Walther F (eds), *The behavior of ungulates and its relation to management*. IUCN, Morges, Switzerland, pp. 477–487.
- Franklin WL (1982) Biology, ecology and relationship to man of the South American camelids. In: Mares M, Genoways H (eds), *Mammalian biology in South America*, Pymatuning Laboratory of Ecology Special Publication, 6. University of Pittsburgh, Linesville, pp. 457–489.
- Franklin WL (1983) Contrasting sociecologies of South America's wild camelids: the vicuña and the guanaco. In: Eisenberg JF, Kleiman DG (eds), *Advances in the study of mammalian behavior*, Special Publication of American Society of Mammalogists 7, Stillwater, Oklahoma, pp. 573–629.
- Galimberti F, Boitani L, Marzetti I (2000) The frequency and costs of harassment in southern elephant seals. *Ethology, Ecology and Evolution* 12:345–365.
- Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WL (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature* 412: 436–438
- Glade CA, Cattán P (1987) Aspectos conductuales y reproductivos de la vicuña. In: Torres H (ed), *Técnica para el manejo de la vicuña*. IUCN/CSE, PNUMA, Santiago, Chile, pp. 89–107.
- Jouany JP (2000) La digestion chez les camélidés; comparaison avec les ruminants. *INRA Productions Animales* 13:165–176.
- Kadwell M, Fernández M, Stanley H, Baldi R, Wheeler J, Rosadio R, Bruford M (2001) Genetic analysis reveals the wild ancestors of the llama and the alpaca. *Proceedings of the Royal Society of London B* 268:2575–2584.
- Koford CB (1957) The vicuña and the puna. *Ecological Monographs* 27:153–219.
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford.
- Lichteinstein G, Vilá BL (2003) Vicuña use by Andean communities: an overview. *Mountain Research and Development* 23:198–202.
- Lopez A, Maiztegui J, Cabrera R (1998) Voluntary intake and digestibility of forages with different nutritional quality in alpacas (*Lama pacos*). *Small Ruminant Research* 29:95–301.
- Lucherini M (1996) Group size, spatial segregation and activity of wild sympatric vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*. *Small Ruminant Research* 20:193–198.
- Lucherini M, Birochio DE (1997) Lack of aggression and avoidance between vicuña and guanaco herds grazing in the same Andean habitat. *Studies of Neotropical Fauna and Environment* 32:72–75.
- Lucherini M, Birochio DE, Marinelli C, Legato AM (2000) Spatial niche overlap between vicuñas and guanacos. *Acta Theriologica* 45: 57–70.
- Ménard N (1982) Quelques aspects de la socioecologie de la vicogne *Lama vicugna*. *Revue Ecologique (Terre et Vie)* 36:15–35.

- Ménard N (1984) Le régime alimentaire des vicognes (*Lama vicugna*) pendant une période de sécheresse. *Mammalia* 48:529–539
- Pfister JA, San Martín F, Rosales L, Sisson DV, Flores E, Bryant FC (1989) Grazing behaviour of llamas, alpacas and sheep in the Andes of Peru. *Applied Animal Behaviour Science* 23:237–246.
- Reiner RJ, Bryant FC (1986) Botanical composition and nutritional quality of alpaca diets in two Andean rangeland communities. *Journal of Range Management* 39: 424–427.
- Renaudeau d'Arc N, Vilá BL (1998) Some aspects of vicuña *Vicugna vicugna* behaviour in Laguna Pozuelos, Jujuy, Argentina. *Proceedings of the 2nd World Conference of Mountain Ungulates*, St. Vincent, Italy, pp. 191–196
- Renaudeau d'Arc N, Cassini MH, Vilá B (2000) Habitat use by vicuñas (*Vicugna vicugna*) in the Laguna Blanca Reserve (Catamarca, Argentina). *Journal of Arid Environments* 46:107–115.
- San Martín F, Bryant FC (1989) Nutrition of domesticated South American llamas and alpacas. *Small Ruminant Research* 2:191–216.
- Sponheimer M, Robinson T, Roeder B, Hammer J, Ayliffe L, Passey B, Cerling T, Dearing D, Ehleringer J (2003) Digestion and passage rates of grass hays by llamas, alpacas, goats, rabbits, and horses. *Small Ruminant Research* 48:149–154.
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, New Jersey.
- Sutherland WJ (1996) *From individual behaviour to population ecology*. Oxford University Press, Oxford.
- Trivers RL (1985) *Social evolution*. Benjamin Cummings, Menlo Park, California, pp 461
- Van Saun RJ (2006) Nutrient requirements of South American camelids: a factorial approach. *Small Ruminant Research* 61:165–186.
- Vilá BL (1990) El comportamiento de la vicuña durante la temporada reproductiva. Unpublished Doctoral Thesis, FCEyN, Universidad de Buenos Aires, Argentina.
- Vilá BL (1994) Use of dung piles by neighbouring vicuñas. *Zoologisch Saugetierkunde* 59:126–128.
- Vilá BL (1995) Spacing patterns within groups in vicuñas, in relation to sex and behaviour. *Studies on Neotropical and Environment* 30:45–51
- Vilá B (2000) Comportamiento y organización social de la vicuña. In: González B, Bas F, Tala C, Iriarte A (eds), *Actas del Seminario Internacional de "Manejo sustentable de la vicuña y el guanaco"*. Servicios Agrarios y Ganaderos de la Universidad C, Católica de Chile, Santiago de Chile, Chile, pp. 175–191.
- Vilá BL, Cassini MH (1993) Summer and autumn activity patterns in the vicuña. *Studies on Neotropical and Environment* 28: 251–258
- Vilá BL, Cassini MH (1994) Time allocation during the reproductive season in vicuñas. *Ethology* 97:226–235
- Vilá BL, Roig VG (1992) Diurnal movements, family groups and alertness of vicuña (*Vicugna vicugna*) during the late dry season in the Laguna Blanca Reserve (Catamarca, Argentina). *Small Ruminant Research* 7:289–297.
- Villalba L (2003) Uso de hábitat e interacciones entre la vicuña y la alpaca en la reserva nacional de fauna Ulla Ulla, Bolivia. In: CIF, FCAyP-UMSS (eds), *Memorias del III Congreso Mundial sobre Camélidos*, 1er. Taller internacional de DECAMA, Vol I., Potosí, Bolivia, pp. 205–210.
- Wilson EO (1980) *Sociobiología. La nueva síntesis*. Omega, Barcelona, Spain.