The distribution and feeding strategy of guanacos in the Argentine Patagonia: a sheep - dependent scenario

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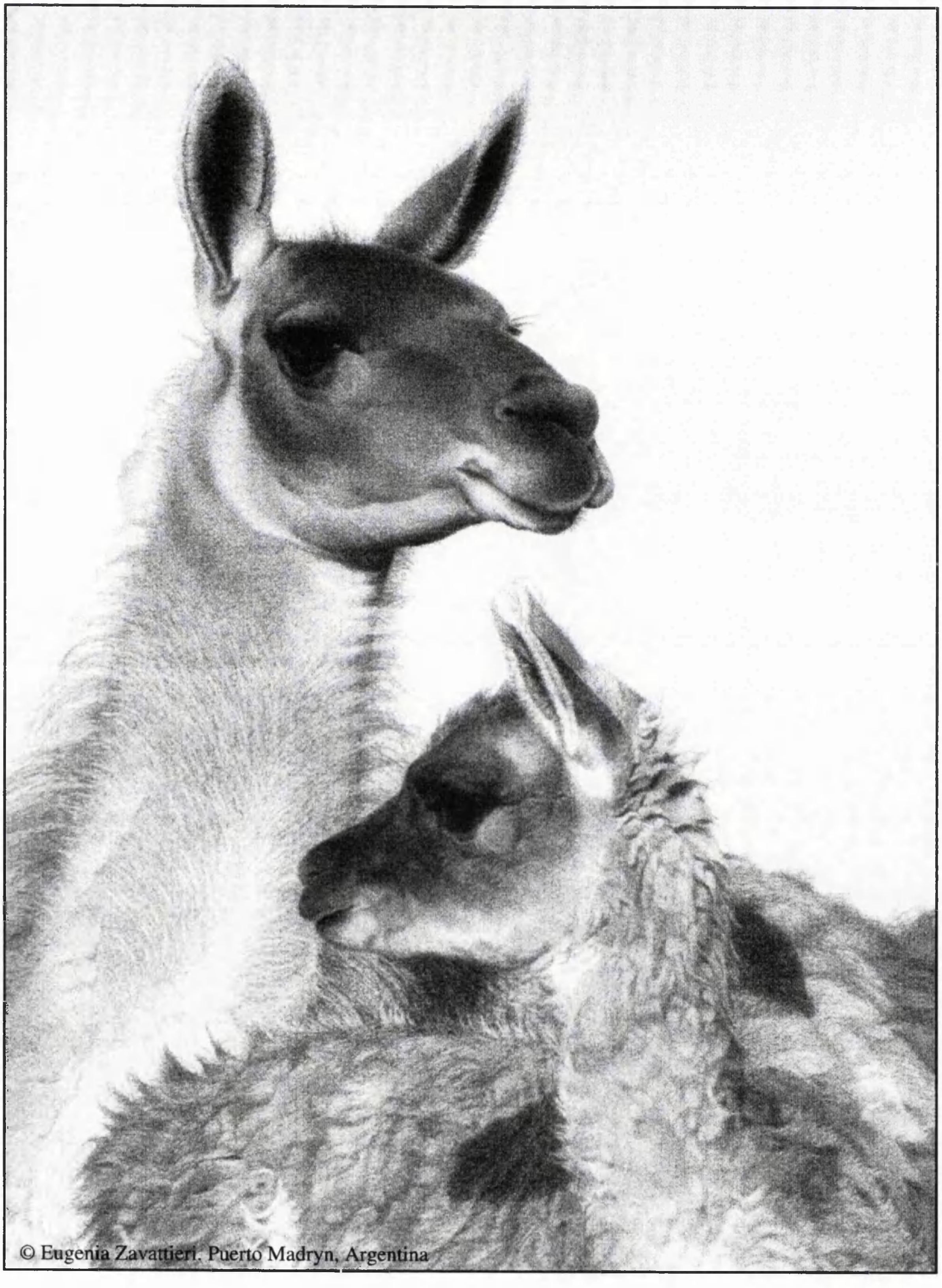
September 1999



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ABSTRACT

In this thesis, I study the feeding ecology and distribution of the guanaco (Lama guanicoe) and the domesticated sheep in the arid-lands of the Argentine Patagonia. First, I review the animal and environmental factors influencing herbivore foraging behaviour. Second, I concentrate on the association between guanaco and sheep densities in relation to food availability. I conducted replicated ground surveys of guanaco and sheep numbers in nine different sites, during two austral summers and one spring. Also, I conducted vegetation surveys and collected faeces to assess diet composition. I found that guanacos are not "browsers" and sheep are not "grazers" but both are "intermediate" feeders in terms of their foraging strategy. Guanacos and sheep have similar diets and show similar patterns of plant species selection. Food niche overlap between guanacos and sheep increased from spring to summer, as forage plants became scarcer in the environment, suggesting a potential for interspecific competition. The distribution of guanacos across sites was inversely related to the availability of the most important plant species in the diet of both guanacos and sheep. In contrast, I found a positive association between sheep densities and the availability of key plant species in the diet. Sheep densities were up to an order of magnitude higher than guanaco densities in sites where both species live sympatrically. Sheep densities accounted for most of the spatial variation in guanaco densities. Furthermore, within-site variation between seasons in guanaco densities were negatively related to changes in sheep densities. Since both herbivores selected a similar diet, the negative correlation between guanacos and sheep cannot be the result of fundamental differences in preferred food resources. These results suggest that interspecific competition may be occurring, and may have played a role in the marked decline of guanaco population during the last 100 years since the introduction of domestic sheep.

ACKNOWLEDGEMENTS

It would have been impossible to put two ends of the world together to do this thesis, had not been for the help and support provided by so many people, here and there. My study in the United Kingdom was funded through a British Chevening Scholarship by The British Council. I am deeply grateful to David Reddaway and Frances Evans at the British Embassy in Buenos Aires. The Wildlife Conservation Society has funded the fieldwork in Patagonia through its Research Fellowship Programme. I want to express my thankfulness to Guillermo Harris and Claudio Campagna. They have been especially influential since early in this process, encouraging and supporting me in many ways.

Once in Britain, Steve Albon became a real person to me after being a faraway author of a very famous book. Steve, I feel I have improved considerably during this time. I am pleased to have been your student, and I am proud of it. Also, many thanks to you and Mary for helping and supporting me beyond the academic life. I thank my UCL supervisor Adrian Lister for his kindness and willingness to deal with my rather tight schedule.

I continue this section by country and subject, in order to avoid omissions.

Argentine crew

For their invaluable assistance and endurance with the fieldwork in Patagonia, a million thanks to Alejandro Carribero, Silvina Vandermolen, Sebastian Cévoli, Fernando Baldi, David Galván, Louise Amos, Rolando González, Julieta Rajlevsky, Laura Biscayart and José Cambareri. The Tourist Office (NATURATUR) in Chubut has provided the authorisation to work in the Cabo Dos Bahías Reserve. I thank the warden Jorge López Cross and his wife Delia for doing always their best to make things easier in the field. I thank the Wildlife Office in Chubut for providing the authorisation to work on the guanacos. To the landowners and workers in the *estancias* where this study was conducted, for their help and interest in my work, thank you very much indeed.

Fundación Patagonia Natural (FPN) was deeply involved with this project, either by taking part in the conservation action or providing logistic assistance with the fieldwork. It is good to know FPN is still committed to underpin the management implications coming up from this work.

The Centro Nacional Patagónico (CENPAT) in Puerto Madryn allowed me to use the lab and computing facilities. Many thanks to Sergio Saba, Mónica Bertiller, Any Beeskow, Daniel de Lamo, Renato Mazzanti, Mateo Cornejo and Fernando Jaguer. Special thanks to Alejandro Bisigato (CENPAT) for being always ready to help with my poor understanding of plant ecology. Marina Stanganelli identified the plant species collected in the field at the Museo de Ciencias Naturales de Puerto Madryn. Alicia Pelliza-Sbriller at the National Institute of Agropecuarian Technology (INTA) in Bariloche conducted the painful analysis of hundreds of guanaco and sheep faeces.

Eugenia Zavattieri kindly allowed me to use her beautiful illustration. The rest of the Argentine crowd I wanted to mention are dear friends who have been especially "close to me" all this time despite the distance: Walter, Analía, Mariana, Valeria, Claudio, Belén, Alejandro and Sebastián.

British crew

I spent my first few months in Britain at the Institute of Zoology in London. I want to thank the people there for making easier my adaptation to this new, old-world. As I was not *that* far from home, I decided to move to the Northeast of Scotland following my supervisor. When I reached him, I found myself at the Institute of Terrestrial Ecology in The Brathens, near Banchory. ITE has proved to be an excellent environment to work in, by its quality, facilities and the friendship of its people.

I want to thank David Elston for patiently following all my thesis work, providing his expertise in statistics. This work would not be the same without his help. All ITE staff was always willing to help with everything I needed. My deepest thanks to Sarah Wanless and Mike Harris for helping me in everything they could and making me feel at home. Thanks to Rene van der Wal for his advice and comments after reading the whole thesis. Steve Palmer, Audun Stien, Mick Marquiss, David Carrs, Hans Kruuk, Adam Watson, Sue Hartley and everyone ready to help in discussing my work or providing their books and references whenever I needed. Thanks to Denise Wright for her kindness, helping once and again with the computers. Joy Reid convinced the immigration officer at Aberdeen airport that I was a legal alien, and also that I deserved an extension of my visa. Many thanks to Seona McKenzie for being so helpful, and to the rest of the admin staff: Donnie, Shirley, Moira, Rosemary and Claire. Also Doug, Alice and Charly. Thanks to all of them for making everyday life smoother.

Last but by not means least, I want to mention the folks for many things difficult to describe. I felt particularly close to Andrew MacColl, Suki Finney, Richard Smith, Giovanna Massei, Sue Lewis, Jenny Bull and Ray Gani. It was great to meet David Gremillet, Audun Stien, Marianne Sinka, Maddie Thurlow, Fiona, Justin, Adam and Annie. Also, and especially, my best wishes to the next ones submitting their thesis, Isla Graham and Arjun Amar. Thanks to one and all.

The journey has come to an end. Bye for now, Britain, I hope to be back before too long. Now it's time to go back home

The Brathens, September 1999

This thesis is dedicated to my family

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Chapter 1. GENERAL INTRODUCTION

1.1 INTRODUCTION

The distribution of ungulates is the result of interacting animal and environmental factors (Jarman 1974, Gordon 1989b, 1989c, 1997). Body size, (Bell 1969, 1970, Jarman 1974, Demment and Van Soest 1985), mouth structure (Gordon and Illius 1988, Janis and Erhardt 1988), gut morphology and function (Hofmann 1973, 1989), sex and reproductive state (Clutton-Brock and Harvey 1983, Osborne 1984), have all been subject of research on the factors influencing foraging behaviour. These animal factors interacting with environmental (i.e. non-animal) factors, like spatial and temporal heterogeneity in food availability, affect resource use by ungulates and therefore their distribution in the environment (Jarman 1974, Owen-Smith 1982, White 1983, McNaughton 1983, Gordon 1989a, 1989b, Owen-Smith 1992, Murray and Brown 1993). In addition, competition and coexistence with other herbivores and predation have all been claimed to be important in shaping ungulate distribution and abundance (Sinclair 1979, 1985, Belovsky 1986, Putman 1996).

In this thesis, my principal aim is to investigate the factors affecting the distribution of guanacos (Lama guanicoe Müller, Camelidae, Tylopoda) in Patagonia, southern Argentina, and in particular their interaction with the domestic sheep (Ovis aries L., Bovidae, Ruminantia) in relation to forage resources. In this chapter, I will set the context for the study by reviewing the animal factors influencing the foraging ecology of ruminants, particularly the morphology of the digestive system and the role of body size and incisor arcade breadth (IAB) in relation to different feeding strategies.

Also, I will review the environmental factors influencing ungulate distribution. In particular, I will concentrate on the variation of food resources in space and time, in terms of forage availability. I will associate this variation in the environment with resource utilisation in ungulates, reviewing some examples in different ecosystems. Next, I will look at the role that interspecific interactions, in particular competition, may play in structuring ungulate communities and how this subject was approached from different studies. Finally in the last section of this chapter, I will provide the framework for assessing the role of competition between guanacos and the other large herbivore sharing their range, the domestic sheep.

1.2 ANIMAL FACTORS

It has been argued that the most important difference separating species of ruminants is their adaptation to consume different diets (Hofmann 1973, 1989). In their classification of African ruminants, Hofmann and Stewart (1972) described three different feeding strategies: (1) bulk and roughage feeders or "grazers" (diet of primarily monocotyledoneous, grasses and graminoid plants), (2) concentrate selectors or "browsers" (diet of dicotyledoneous, woody and herbaceous plants) and (3) intermediate feeders, which include a mixture of monocots and dicots in their diets (Table 1.1). These adaptations can be related to differences in the properties of the foliage of monocotyledoneous (monocots) and dicotyledoneous plants (dicots). It is known that dicotyledoneous plants have higher levels of cell solubles and crude protein but lower levels of holocelullose than grasses (Demment and Van Soest 1985, Owen-Smith 1997). Consequently, dicots have higher levels of rapidly fermenting soluble

Table 1.1: Summary of morphologic adaptations in the digestive system of ruminants to different diets and their associated functions, as proposed by Hofmann (1973, 1989). *SCFA:* short-chain fatty acids.

BULK/ROUGHAGE EATERS (Grazers)	**CONCENTRATE SELECTORS (Browsers)**	**INTERMEDIATE FEEDERS**
Stomach structure		
(1) large, dorsally attached ruminureticulum (2) narrow ostium intraruminale (3) small ostium (4) large omasum (5) small reticulum	(1) small, dorsally unattached ruminureticulum (2) wide ostium intraruminale (3) large ostium (4) small omasum (5) large reticulum	Structure resembles those of browsers (simple type), although capacity is variable across the group, with some structures of "medium size"
(6) uneven rumen papillation, with unpapillated zones	(6) even, dense rumen papillation	seasonal, partial calcification of the rumen papilla seasonal changes in the mucosa surface
Associated functions		
(1): maximise food retention time and cellulolytic fermentation (2) and (3): slow passage of ingesta within the stomach. (1) and (5): slow contractions allowing stratification of rumen contents (4): water absorption (6): slow absorption of SCFA	(1): minimise food retention time and maximise cell content fermentation. (2) and (3): rapid passage of ingesta within the stomach. (1) and (5): fast and complete contractions and fast turnover of ingesta (4): prevents unchewed leaves to enter to the abomasum. (6) fast absorption of SCFA	seasonal adaptations to changes in the diet in terms of proportions of monocots and dicots available
Hindgut structure		
(1) small intestine represents 80-82% of the hindgut length (2) short spiral colon	(1) small intestine represents 65-73% of the hindgut length (2) long spiral colon	Similar to browsers
Associated functions		
nutrient absorption	delay food passage continuing fermentation and absorption	Similar to browsers
Examples		
African ruminants Oryx, Topi, Wildebeest, African buffalo, Waterbuck	Dikdik, Duiker, Kudu, Giraffe	Impala, Thomson gazelle, Eland antelope
European ruminants Mouflon, Cattle, Sheep	Roe deer, Moose	Reindeer, Red deer, Goat, Ibex

components than grasses. However, because of their higher lignin contents in the cell - wall, the absolute digestibility of browse tends to be lower than grasses (White and Trudell 1980). Therefore, browsers are thought to have a digestive system adapted for the rapid excretion of highly lignified parts of the cell wall of dicots. Whereas, grazers have adaptations in the rumen to slow down the passage of plant material and to increase the extent of digestion of the less lignified cell wall component of monocots (Hofmann 1973, 1989).

Hofmann (1973) hypothesised that anatomical adaptations of the alimentary tract were related to feeding habits, showing that grazers have larger, less subdivided and more muscular stomach than browsers. He argued that this was an effective strategy for using the large amount of digestible cell wall in grasses (Table 1.1). Even though there is a tendency for small species to be browsers and large species to be grazers (Jarman 1974, Case 1979), Hofmann (1989) stressed the importance of digestive adaptations as the dominant factor affecting feeding habits, independently of body size.

An alternative hypothesis to account for the diversity of ungulate feeding strategies was proposed by Jarman (1974), based on earlier work by Bell (1969, 1970). In a classic study of the ecology of the 74 species of African antelope (African Bovidae), Jarman described five feeding categories based on the dispersion and availability of forage species, monocotyedoneous and dicotyledoneous plants, in the environment (Table 1.2). He found a general, inverse relationship between body size and selectivity, with the animals below 50 kg body weight tending to be highly selective (browsers) in terms of plant species and parts. In contrast, the largest animals above 200 kg) fed unselectively, primarily on grasses. Between these extremes, Jarman (1974) found a range of intermediate selectivity, with animals feeding on browse and grass in

Table 1.2: Summary of the relationships between body weight, feeding style, diet and food quality and distribution proposed by Jarman (1974) for African antelope species. Body weight ranges are approximate.

BODY WEIGHT (kg)		FEEDING STYLE	DIET & DISPERSION OF FOOD ITEMS	Examples
4 – 20	(a)	Very selective feeding on a wide range of plant species, using particular plant parts only. Browsers. Small home range.	Flowers, twig tips, fruits, seed pods, bark. Food items of high nutritive value. Food items spatially scattered.	Duikers, Dik-dik, Grysbok, Steinbok, Suni
20 – 80	(b)	Species feeding either entirely on grass OR entirely on browse plant species. Very selective for plant parts. One home range throughout the year.	Range of grasses or browse. Diet show some seasonal variation. Food items of high nutritive value. Dispersion of food items is intermediate between (a) and (c).	Bohor, Reedbuck,Bushbuck, Oribi, Gerenuk
50 – 200	(c)	Species feeding on a range of grass AND browse, rather selectively, on a range of vegetation types. Large home area.	Range of grasses and browse. Diverse, seasonally changing diet, usually including more grass during the wet season and more browse during the dry season. Feeding behaviour typically flexible. Food distribution in space is more 'continuous' than that for style *a*.	Waterbuck, Gr. Kudu, Impala, Grant's and Thomson's gazelles, Nyala
140 – 220	(d)	Species feeding on grasses, more selective for plant parts than for plant species. They may migrate to find grasses at optimum growth stage. Poorly defined home area.	Grasses. Diet of very low diversity. Low nutritive value of food items compared with feeding styles (a) and (b). Food distribution is highly contrasting to that of style (a). Optimum grass growth is distributed continuously within a region, but non-synchronised with other regions.	Wildebeest, Hartebeest, Topi
200 – 700	(e)	Species feeding on a large range of grasses or grass and browse. Feeding is non selective for plant parts or species. They move seasonally within a very large home area.	Diverse diets. Food items may be quite low in nutritive value. Dispersion of food items is rather continuous.	Buffalo, Eland

important proportions, associated with an intermediate range of body weight (50-200 kg) (Table 1.2). These findings suggested that small animals need high quality food, in terms of nutritive value and digestibility, because their energetic requirements are relatively high compared to large animals.

Since gut capacity scales isometrically with body weight ($W^{1.0}$) and metabolic requirements are related to $W^{0.75}$, Bell (1969, 1970) and Jarman (1974) argued that small animals have higher metabolic requirements per unit body weight than large ones. Also, this implies that large animals are able to tolerate diets of lower digestibility than small animals, while the smaller species are constrained to feed selectively on higher quality diets. This negative relationship between selectivity and body size was explained by looking at the variation in mouth structure across a body size gradient. By comparing data on 89 species of ruminants, Gordon and Illius (1988) found that incisor arcade breadth (IAB) increases with body size ($IAB = 6.36\ W^{0.40}$). In addition, after taking into account the different feeding habits of different species, Gordon and Illius (1988) found that grazers have a significantly wider IAB than browsers ($IAB_{grazers} = 8.11\ W^{0.36}$; $IAB_{browsers} = 6.69\ W^{0.36}$). However, there was considerably overlap in the IAB of grazers and browsers below 100 kg body weight, which suggested that all animals below 100 kg are able to be selective to some extent. In contrast, as IAB increases with body size, then selective pressures on the IAB of browsers would increase to sustain a selective feeding strategy (Gordon and Illius 1988). Thus, in practice body size and its associated effects on gut capacity, energetic requirements and mouth structure should all play a part in determining the feeding strategies of ruminants (Illius and Gordon 1987, Gordon et al. 1996, Illius 1997).

Both Hofmann's hypothesis about morphological adaptations of ruminants to the type of diet and Jarman's hypothesis about the role of body size in relation to food quality and dispersion, have stimulated research on the nutritional ecology of ruminants. In a study designed to test specific predictions of Hofmann's hypothesis, the data suggest that there are no significant differences in the digestive function of African ruminants with different feeding habits, after controlling for allometric effects. By modelling data on digestion for 21 species of African ruminants, Gordon and Illius (1994) found no differences in mean retention times in the gut between browsers and grazers after accounting for variation due to body mass and food type. Instead, rumen fermentation rate was found to be higher in smaller animals (Gordon and Illius 1994), and potential digestibility of the diet was negatively correlated with body mass (Gordon and Illius 1996) in accordance with the implications of Bell (1969, 1970) and Jarman's (1974) hypotheses. However, digestibility range was estimated to be remarkably narrow in terms of variation in cell solubles and digestible cell wall (Gordon and Illius 1996). Nevertheless, when the rate of energy assimilation is considered, the multiplier effects of both forage intake and digestion rates results in larger animals achieving the highest energy assimilation, despite their slightly less digestible diet (White 1983, Illius and Gordon 1991, Illius and Gordon 1992). In addition to these problems with Hofmann's hypothesis, Robbins et al. (1995) have found that the extent of fiber digestion did not differ between the three feeding categories proposed by Hofmann and Stewart (1972) but rather, that it was positively related to body size.

In summary, there has been increasing evidence that animal factors such as mouth morphology, gut capacity and digestive function are all related to body size. Consequently, body size should be the dominant animal factor influencing the nutritional ecology and feeding strategies of ruminants (Robbins et al. 1995, Gordon et al. 1996, Illius 1997).

1.3 ENVIRONMENTAL FACTORS

As stated earlier in this chapter (see section 1.1), resource use by ungulates, and therefore, their distribution in the environment, are the result of interacting animal and environmental factors. Not surprisingly, the distribution and abundance of food items in space and time (Jarman 1974, McNaughton 1983, Gordon 1989a, 1989b, Owen-Smith 1992, Murray and Brown 1993) together with interspecific interactions (Sinclair 1979, 1985, Belovsky 1986, Putman 1996) strongly influence resource partitioning within a given ungulate guild.

1.3.1 Variation in forage availability in space and time

Grass and browse forage shows contrasting patterns in space and time, in terms of abundance and quality (Owen-Smith 1982, 1992). Grass tends to be more homogeneously distributed than browse in space, to markedly change its nutritive value seasonally, and also to be more homogeneous in the food value of their plant parts at a given time than browse. In contrast, a proportion of "browse" maintains green leaves over more of the year than grass, and high digestible tissues are restricted to particular plant parts, usually protected against herbivory by structural or chemical components (Jarman 1974, Crawley 1997).

Seasonal and spatial changes in vegetation composition are strongly influenced by climatic variables. For example, in temperate ecosystems temperature influences seasonal cycles in the abundance of live plant material. On the Isle of Rum, Scotland, the biochemical properties and potential digestibility of graminoids, forbs and shrubs eaten by ruminants vary seasonally, with up to eightfold increases in the standing crop during the summer (Gordon 1989a). In tropical savanna ecosystems, seasonal changes in the availability of grass forage are strongly dependent on the seasonal cycle of rainfall (Northon-Griffiths et al. 1975). As ecosystems become increasingly arid, biological processes are primarily controlled by water inputs which are infrequent, discrete and largely unpredictable (Noy-Meir 1973). Some plant life forms, particularly grasses and forbs, are closely associated with these water inputs and therefore restricted to developing in periods when water and nutrients are available in the upper soil layer (Fischer and Turner 1978, Sala et al. 1989). As rainfall regimes vary in space, the transition from semi-arid to arid condition is associated with changes in vegetation composition, from herbaceous to shrub-dominated communities (Reynolds et al. 1997). Even in relatively wet savanna ecosystems like the Serengeti, spatial variation in composition and structure of different grassland communities is strongly associated with mean annual rainfall (McNaughton 1983).

1.3.2 Ungulate resource use in relation to forage availability

Environmental heterogeneity in food availability affects ungulate resource use in space and time and therefore their distribution. Ungulate responses to changes in vegetation composition and forage availability are well documented in the literature. On the Isle of Rum, vegetation communities differed in the abundance of dwarf-shrubs, forbs and graminoids (Gordon 1989a). Accordingly, predominantly grazing species like cattle, ponies and red deer (Cervus elaphus) selected vegetation communities dominated by graminoids and forbs while goats, predominantly browsers, selected dwarf-shrub communities (Gordon 1989b,c). Since the seasonal temperature cycle on Rum results in a substantial variation in food quality (Gordon 1989a), all ungulate species seasonally change vegetation community use. Predominantly grazer species were positively associated with the available biomass across different grass and forb dominated communities, while vegetation use by goats was generally associated with the biomass of heather and forbs (Gordon 1989b). Another strategy to deal with seasonal change is to migrate. For example, in Norway, some red deer females migrate to a higher altitude during summer. Albon and Langvatn (1992) have shown that individual females who migrate have longer access to high quality forage, as winter snow occurs and melt later and retards plant development and its subsequent decline in quality. In the Serengeti-Mara ecosystem, wildebeest (Connochaetus taurinus) seasonal migration is related to the availability of grass, resulting in millions of animals being present in the same place during the same period of time (Sinclair 1979).

1.3.3 Interspecific interactions: competition and coexistence

In addition to forage availability, it was argued that interspecific competition affects community structure (Schoener 1983, Tilman 1987, Hairston 1989, Putman 1996). Potentially competing species should have similar preferences for food resources, they must overlap in habitat use, and food availability must be limited (Belovsky 1986, Wiens 1989, de Boer and Prins 1990, Putman 1996). Within this scenario, competition is expected to result in the exclusion of a species or a change in the pattern of resources used in the presence of another species (Schoener 1974, Belovsky 1984). In contrast, coexistence results from a fundamental difference in resources preferred by two or more species (Krebs 1994, Putman 1996), or when food is not limiting to herbivore populations (Belovsky 1986).

Strong evidence of competition has proved to be difficult to find, as it requires experimental manipulation (Schoener 1983, Hobbs et al. 1996a, 1996b), something which is very difficult to undertake with large herbivores (Gordon and Illius 1989, Putman 1996). Instead, observed patterns of resource use in sympatric and allopatric conditions have been frequently taken as an approach to the study of interspecific competition in ungulates (Sinclair 1979, Sinclair and Norton Griffiths 1982, Sinclair 1985, Gordon and Illius 1989, de Boer and Prins 1990). One problem with this approach is to assess the role of competition when other explanations are plausible (see Wiens 1989). An example of this problem is provided by the long-term studies on the ecology of the Serengeti-Mara ungulate community. After the annual migration of wildebeest, Sinclair (1979) observed changes in resource partitioning patterns of Burchell's zebra (Equus burchelli), topi (Damaliscus korrigum), kongoni (Alcelaphus buselaphus), Thomson's gazelle (Gazella thomsoni), Grant's gazelle (Gazella granti), impala (Aepyceros melampus), waterbuck (Kobus defassa) and warthog (Phacochaerus aethiopicus). Sinclair (1979) found that overlap in habitat selection decreased in the dry season, after five species changed their habitat preferences, as predicted during competitive interactions. However, predation has also been claimed to be important in shaping the Serengeti ungulate community. Both gazelle species were at closer distances to wildebeest than expected and was interpreted as a strategy to decrease the risk of predation (Sinclair 1985). Subsequently, poaching by humans has been considered as a major cause in the decline of some populations of the Serengeti-Mara ungulate guild (Dublin et al. 1990). The Serengeti example illustrates the difficulties of the comparative approach to detect competition, particularly in complex communities.

In another study in northern Tanzania, de Boer and Prins (1990) tested different hypotheses about interspecific interactions between African buffalo (Syncerus caffer), African elephant (Loxodonta africana), zebra and wildebeest. The small habitat overlap between buffalo and elephants in preferred vegetation patches supported predictions on competition, while zebra and wildebeest appear to benefit from "food manipulation strategy" by large buffalo herds, making periodic returns to preferred grass patches (de Boer and Prins 1990). It was argued that buffalo can optimise food quality by choosing the appropriate return time to vegetation patches that have regrown after they were grazed (Prins 1988). Since herds of zebra and wildebeest were observed grazing together with larger buffalo herds, de Boer and Prins (1990) hypothesised that zebra and wildebeest benefited from the association.

On the Isle of Rum, Scotland, grazing species such as red deer, cattle and ponies decreased in habitat overlap during the winter (Gordon and Illius 1989), when both the digestibility and abundance of grass species decreased in relation to summer conditions (Gordon 1989a). In contrast, browsing goats decreased their habitat overlap with the grazing species during the summer, as availability of new shoots on dwarf shrubs increased. Although the decrease in habitat overlap of grazing species is consistent with the hypothesis of competition influencing resource partitioning (Gordon and Illius 1989), grazing facilitation between cattle and red deer was more evident. Gordon (1988) has found that cattle grazing in winter resulted in higher availability of green tissue for red deer during spring, and this was associated with an increase in the number of calves per hind in areas with cattle.

In another study in the western highlands of Scotland, the presence of sheep reduced the use of preferred swards by red deer hinds (Osborne 1984). Furthermore, Clutton-Brock and Albon (1989) found a negative relationship between red deer and sheep across 48 parishes in the Scottish highlands, consistent with the occurrence of competition for some preferred vegetation communities.

Stronger evidence on interspecific competition was obtained in a manipulative study conducted on elk (Cervus elaphus canadensis) and cattle by Hobbs et al. (1996a). This study demonstrated that the standing crop of perennial grass decreased with increasing densities in elk, together with a decrease in digestible food intake by cattle. Moreover, this affected the body mass of cows and their reproductive output leading to the conclusion that elk reduced cattle production under food limiting conditions (Hobbs et al. 1996b).

In summary, the influence of animal and environmental factors on foraging strategies reviewed above, provide the framework for this thesis. The central idea is that the distribution of ungulates is the result of interacting animal and environmental factors. Animal adaptations interacting with forage properties influence ungulate feeding ecology. The variation in food abundance and quality in space and time, and the presence of potential competitors will affect the way the animals use the resources and hence the way they are distributed in the environment.

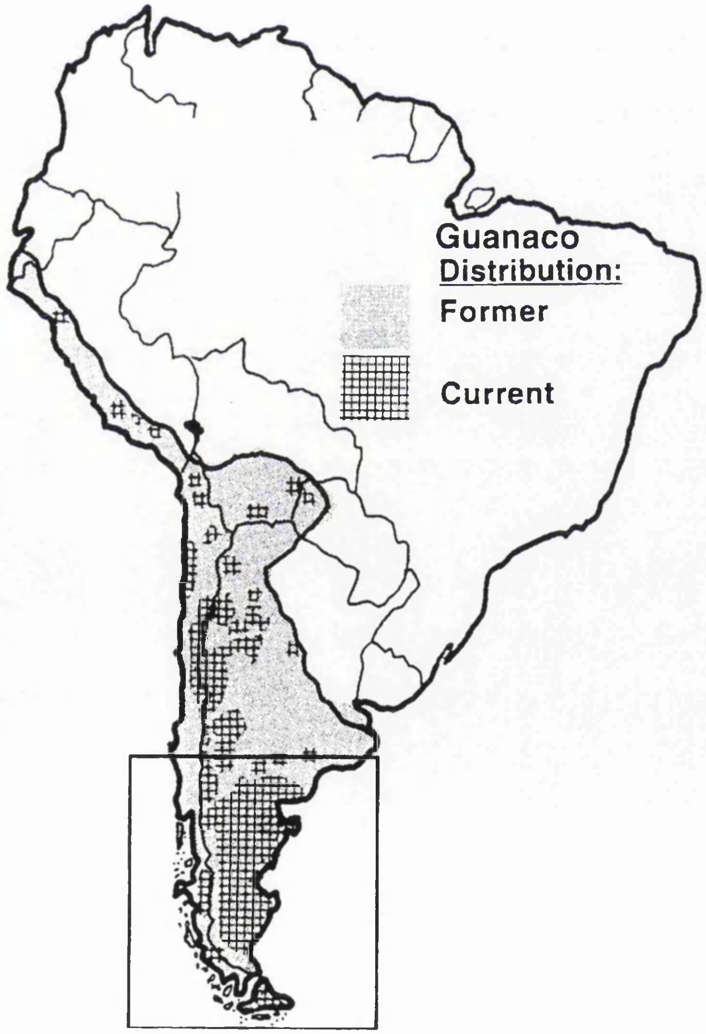
1.4 THE UNGULATES OF PATAGONIA

Guanacos and introduced sheep are the most numerous ungulates in Patagonia, particularly in the large steppe region. Cattle are far less common and restricted to narrow valleys along the main rivers in northern Patagonia. Also, native deer species like the huemul (Hippocamelus bisculus) and the pudu (Pudu pudu) are now very rare and their distribution is associated to the subantarctic Andean forest in western Patagonia.

1.4.1 Guanacos and sheep: animal factors

Guanacos are one of four species of South American Camelids. Unlike llamas (Lama glama) and alpacas (Lama pacos), they have never been domesticated. The fourth species, the vicuña (Vicugna vicugna), is also wild and has a distribution limited to high altitudes in the Andes (Franklin 1982). Guanacos are the only widely distributed, large native herbivore, from Perú to Tierra del Fuego (Franklin 1982, Figure1.1).

Figure 1.1: Past and present distribution of guanacos in South America. Patagonia is the area in the rectangle (taken from Franklin et al. 1997).



Adult guanacos weigh 90-120kg and are not sexually dimorphic in body size (Raedeke 1979, Franklin 1982). Like other camelids, guanacos show some morphologic adaptations expected to favour selective feeding strategies. Camelids are not "true ruminants", but are functionally ruminants since plant fermentation takes places in the foregut and they remasticate the cud (Heller et al. 1984). All camelids have high gut motility and high rates of passage of food relative, to sheep and cattle (Maloiy 1972, Hintz et al. 1973) in accordance with Hofmann's (1973) description for concentrate selectors (see Table 1.1). For example, the frequency of forestomach contractions in llamas are substantially higher than in sheep, which allows a high mixing of food with bicarbonate buffer (Heller et al. 1984). Also, the two stomach compartments analogous to the reticulorumen of ruminants are smaller in llamas than in sheep (San Martin 1987). Moreover, absorption rates of water and solutes in South American camels was reported to be 2 – 3 times higher than in the omasum of sheep (Rubsamen and Engelhardt 1978). In addition to the morphology and function of the digestive system, Camelids have a relative narrow muzzle, bifid upper lip and a mobile tongue (Mukasa-Mugerwa 1981, Janis and Ehrhardt 1988). However, although guanacos should be browsers according to their digestive system and mouth structure (IAB = 31.4 mm S.E. = 1.7, n = 8 adult females; Baldi, unpublished data), they have been consistently described as intermediate feeders, able to change the proportion of browse and grass in their diet (Dennler de la Tour 1954, Balmaceda and Digiuni 1979, Raedeke 1980, Bahamonde et al. 1986, Cajal 1989, Bonino and Sbriller 1991). Other camelids including the domestic llama, alpaca, and the bactrian camel (Camelus bactrianus), have all been classified within the intermediate feeders category (Van Soest 1994, Janis and Ehrhardt 1988), while dromedary camels (Camelus dromedarius) have also been described as both intermediate feeders and browsing specialist (Coppock, Ellis and Swift 1986, Coppock, Swift and Ellis 1986). In contrast, Vicuñas (45 – 55 kg body weight) feed predominantly on grasses and forbs, although they are very selective feeders in terms of plant species and parts (Franklin 1983) resembling those species described in feeding style "b" by Jarman (1974).

Adult domestic sheep of the Merino variety introduced to Patagonia typically weigh between 50 and 80 kg. According to Hofmann (1973, 1989), sheep have a relatively big reticulo-rumen in terms of capacity and weight, a low fermentation rate, a small ostium reticulo-omasicum that retards the passage of ingesta from the rumen, and uneven papillation size and distribution in the rumen. Mean retention time in the reticulo-rumen of sheep was reported to be substantially higher than in goats and red deer (Van Soest 1994). Incisor arcade breadth for sheep was estimated to be 32 mm (Gordon and Illius 1988), close to the predicted IAB for grazers of 50 kg. However, since sheep body weight is well below 100 kg they are expected to be selective (Gordon and Illius 1988). Although sheep have been classified as grazers (Hofmann 1989) and indeed they can include a high proportion of monocots in their diet (Grant et al. 1985, Hodgson et al. 1991), sheep were also described as intermediate feeders (Coppock, Ellis and Swift 1986, Edwards et al. 1995).

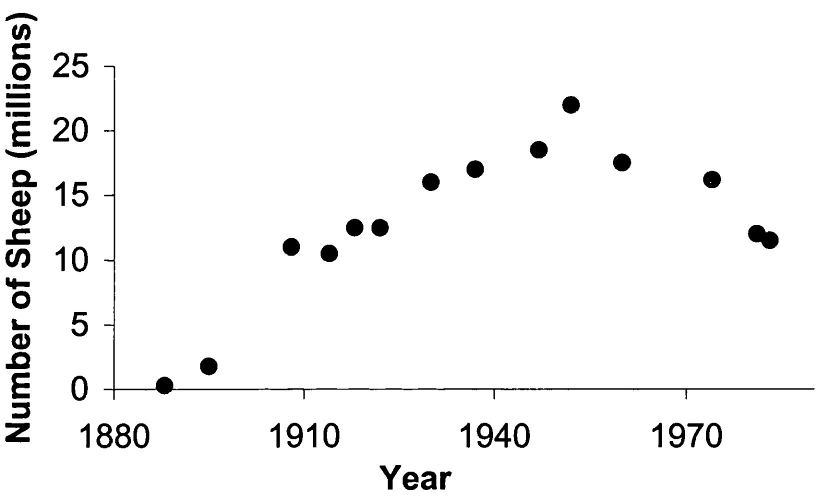
1.4.2 Guanaco population trends

Guanacos were the only ungulate species inhabiting the Patagonian steppe from the end of the Pleistocene (10,000 – 12,000 years ago) until the introduction of domestic livestock (Franklin 1982). The aboriginal population of guanacos was estimated to be in the range of 30 to 50 million (Raedeke 1979), but during the period of European colonisation the population must have declined severely (Franklin and Fritz 1991). Early naturalists and travellers in South America gave accounts that suggested guanacos were extremely abundant. Darwin (1845) stated that guanacos were "very common over the whole of the temperate parts of the continent". He saw herds of up to 500 individuals on the shores of Santa Cruz River in Southern Patagonia. Musters (1871) recorded seeing herds composed of three or four thousand individuals, and Prichard (1902) wrote that "literally thousands appeared on the summits of the surrounding ridges". By the end of the last century, some estimates suggest that about seven million guanacos still remained (Cabrera and Yepes 1940, Torres 1985).

Today guanacos are still the most numerous and widely distributed of the South American Camelids (Redford and Eisenberg 1992, Franklin et al. 1997) but have continued their precipitous decline (Figure 1.1). The causes of this decline are unknown but over-hunting and range degradation due to overstocking with sheep may have played a role (Raedeke 1979, Franklin 1982, Cunazza et al. 1995). Today, the guanaco occupies only 40% of its original range (Puig 1995, Franklin et al. 1997). In addition, the present distribution has become fragmented into smaller, relatively isolated populations. Although the species is not threatened with extinction at a continental scale, some populations are under serious risk of local or even regional extirpation (Cunazza et al. 1995). Now, 96% of the guanaco population is thought to occur in Argentina (Franklin 1982, Torres 1985), mainly in Patagonia (Figure 1.1). Nevertheless, their distribution is poorly documented and estimates of abundance are scarce, even in protected areas (Puig 1992, Baldi et al. 1997).

It has been argued that today guanacos might be occupying marginal habitats of low productivity, as a result of sheep grazing (Puig 1995). Extensive sheep grazing is now the dominant farming activity over almost 600,000 km^2 of Patagonian steppe. Sheep were introduced in large numbers towards the end of the 19th century, reaching a peak of 22 million during the 1950's (Soriano and Movia 1986, Figure 1.2).

Figure 1.2: Number of sheep in the Argentine Patagonia since they were introduced in about 1890 (data from Soriano and Movia 1986).



Nevertheless, no previous studies have been designed to investigate the effect of sheep on guanaco distribution in Patagonia. Although there have been a few studies of guanaco diet, most have not considered food availability (Puig 1995). Even fewer studies have investigated the presence of sheep and their diet selection within guanacos range, usually because guanacos have been studied in protected areas where sheep are excluded (Cajal 1989, Puig et al. 1996, Franklin 1983, Ortega and Franklin 1988). Clearly an evaluation of the dietary overlap between guanacos and domestic livestock is required to assess the extent to which sheep might be adversely affecting guanaco habitat utilisation and population decline (Puig et al. 1997).

In summary, available data on guanaco population numbers and distribution is scarce and outdated. Also little is known about how different habitats and sheep densities affect the distribution of guanaco subpopulations in Patagonia. Therefore, baseline ecological data is needed to develop a management plan for guanacos, and essential for the long-term conservation and sustainable use of this species (Torres 1995).

1.5 GENERAL HYPOTHESES

The knowledge of how animal and environmental factors interact and influence herbivore foraging (reviewed above) enables me to make the following general hypotheses:

1. If the adaptations in the digestive system determine feeding strategies as proposed by Hofmann (1973, 1989), then guanacos will be predominantly browsers and sheep predominantly grazers. In contrast, if body size and its associated correlates are of major importance in shaping the feeding strategies as proposed by Jarman (1974) and others (see section 1.2 above), then both guanacos and sheep will be intermediate feeders (feeding category "c" in Jarman's terms, Table 1.2), but guanacos will be able of including a higher proportion of grasses than sheep in their diet.

2. If guanacos and sheep differ in their foraging strategies and food preferences, then the distribution of guanacos will primarily depend on the abundance of preferred forage and not on sheep distribution. In contrast, if body size and its correlates are determinant of guanaco and sheep feeding strategies, there will be a high potential for interspecific competition for food resources (Schoener 1974, Belovsky 1986, Gordon 1989c, Putman 1996). Therefore, guanaco distribution will be strongly dependent on sheep densities rather than on the availability of preferred forage.

1.6 APPROACH OF THIS STUDY

The general hypotheses outlined above were approached from a geographical, comparative perspective, rather than using specifically designed experimental manipulations. This reflects a number of priorities and constraints at the time the research programme was established. First, given the poor state of knowledge on guanaco basic ecology, I decided to tackle very basic questions about the main factors shaping their distribution that provide baseline information for future, more detailed research. Second, since the range of guanaco distribution in Patagonia is very large (more than twice the area of the United Kingdom), it was necessary to invest effort in accounting for some of the geographical variation in environmental conditions in an attempt to draw more general conclusions. Third, the lack of information on guanaco population densities and distribution made it essential to obtain reliable estimates that can be easily repeated and extended in the future. This should underpin guanaco population assessment aiming to improve current management conditions. In addition, some constraints associated with the sponsorship of this study made it necessary to maximise the amount of information obtained during relatively short field sessions. These limitations were mainly due to the British Council regulations, which did not allow me to receive my stipend while outside the United Kingdom. As a result, I was not able to spend as much time as I would have liked in the field in Argentina and therefore it was not feasible to conduct experimental manipulations.

1.3 THESIS STRUCTURE

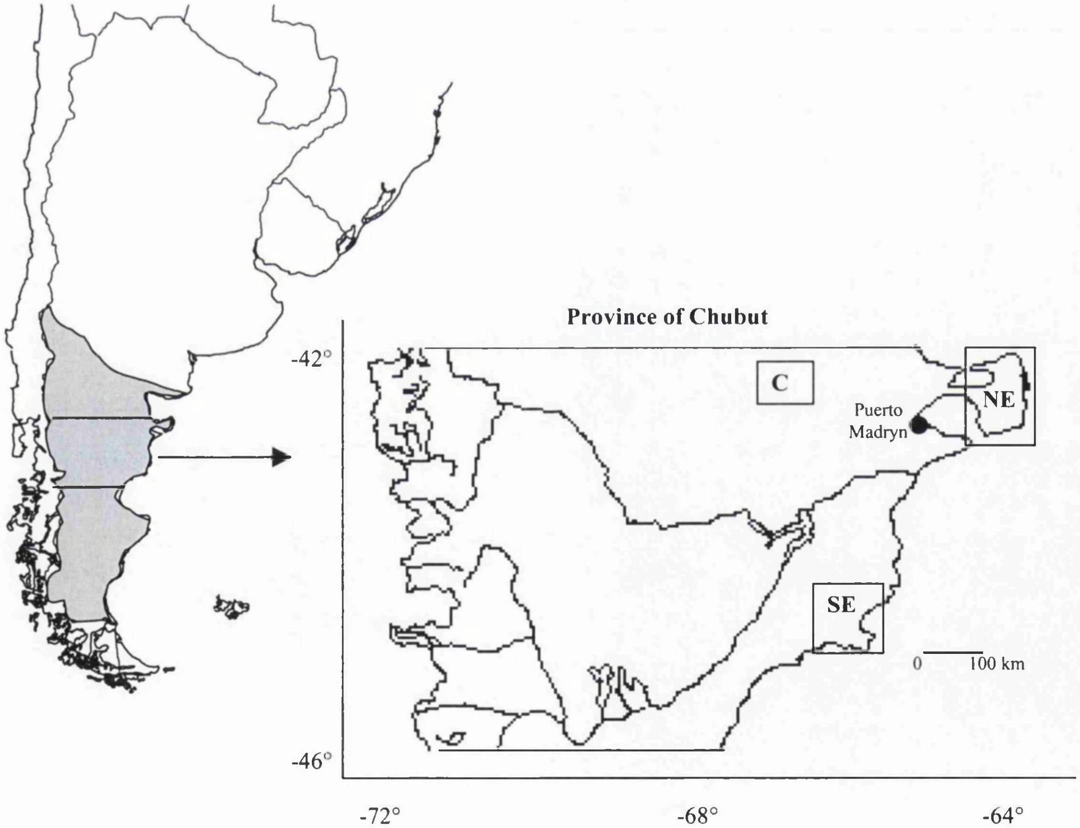
In the next chapter, I describe in detail the study area in Patagonia and more briefly the general methodology of estimating animal densities and vegetation composition (*Chapter 2*). In *Chapter 3*, I show how vegetation composition varies in time and space in my study area. The animal factors discussed in this general introduction (see above) generate specific predictions about guanaco and sheep feeding strategies, which are tested in *Chapter 4*. In *Chapter* 5, I analyse the distribution of guanacos in space and time in relation to sheep densities and vegetation composition. I do this at two different scales, a regional and a local scale during different seasons, the austral summer and spring. Finally, I discuss the main results in *Chapter 6* within the context of the animal and environmental factors affecting the feeding strategies and resource use in ungulates, and in particular the role that interspecific competition with sheep and human activities may have played in shaping the current guanaco distribution. I conclude by discussing the requirements for further research on guanacos and giving some recommendations aiming to improve the current management conditions.

Chapter 2. GENERAL METHODOLOGY

2.1 THE STUDY AREA

The study was conducted in the Province of Chubut, Argentine Patagonia (Figure 2.1) during two austral summers (December 1996 – February 1997 and December 1997 – March 1998) and one spring (September – November 1997).

Figure 2.1: Location of regions in the study area, Chubut, in the Argentine Patagonia (shaded area). NE: Northeast region (4 sites), SE: Southeast (3 sites) and C: Central region (2 sites).



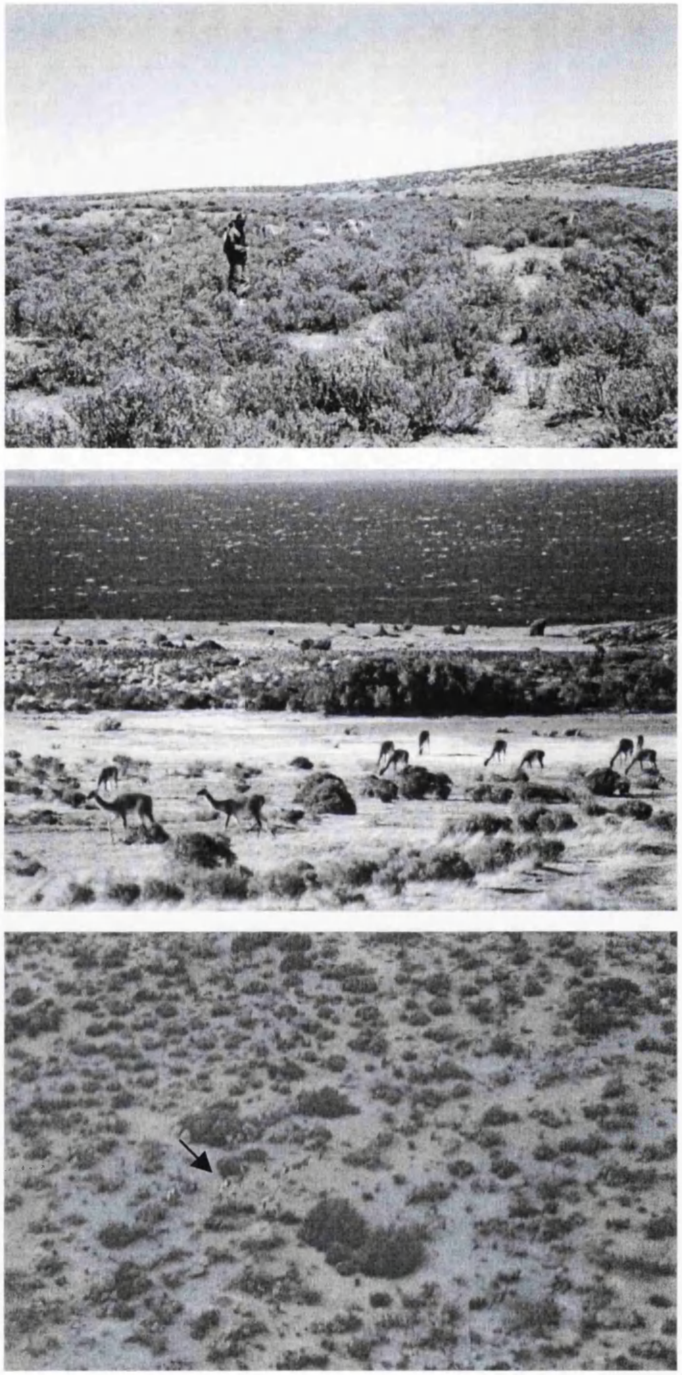
2.1.1 Location and climatic variables

Three different geographical regions where selected within Chubut (Figure 2.1): (a) the North East region, with 4 adjacent sites in Península Valdés (sites 1-4); (b) the South East region, with 3 sites (5-7) including a 1,200 hectares wildlife reserve; and (c) the Central region, comprising 2 sites (8,9). All sites are situated on the arid and semi-arid Patagonian steppe.

The most distinctive climatic factor across the area is the low rainfall associated with a high interannual variation. Although there is no marked rainy season, most of the rainfall occurs during the autumn and winter (March to August) (Barros and Rivero 1982). Average annual rainfall for the NE region is 210mm (ranging between 200-225 mm across the Península Valdés) (CV = 40%), 250 mm (CV = 26%) for the SE and 125 mm (CV = 50%) for the Central region (Beeskow et al. 1987). These rainfall regimes would be classified as arid and semi-arid zones using the UN criteria based on the relationship between precipitation (P) and potential evapotranspiration (PET). Sites 8 and 9 in the Central region belong to the lower - arid zone ($P/PET<0.20$); sites 1 and 2 belong to the upper - arid ($0.20<P/PET<0.30$); and sites 3, 4, 5, 6 and 7 to the lower - semiarid zone ($0.30<P/PET<0.50$) (Beeskow et al. 1987).

Mean annual temperature is 12.2°C in the NE area, 12.8°C in the SE and 12.9°C in the Central region. For all regions, mean temperature ranges between 4-6°C during July and between 18-21°C in January; whilst absolute temperatures ranged from around -18 to 41°C (data from 1931 to 1970, National Weather Service).

Figure 2.2: The NE region (above), the SE (middle) and an aerial view of the Central region (below, the arrow indicates a group of guanacos).



2.1.2 Vegetation and topographic features

There are two main physiognomies that generally characterise the vegetation of arid and semi-arid Patagonia, these are herbaceous and shrub steppes (Beeskow et al. 1995). Vegetation structure in the Patagonian steppe is highly patchy, with high-cover vegetation patches ranging between 1 and 100 m diameter (Aguiar and Sala 1999), surrounded by areas with a high proportion of bare soil (Bertiller et al. 1991).

At a landscape level, the geographic regions are situated in two major phytogeographic domains, related to precipitation. The NE and SE regions are included in the Patagonian Phytogeographical Province, Central District and San Jorge Gulf District respectively, while the Central region belongs to the Monte Phytogeographical Province (Soriano 1956). (see Figure 2.2 for a view of the study regions).

Principal species representing the Patagonian Province are the shrubs Chuquiraga avellanedae, Lycium chilense, Mulinum Spinosum and Nassauvia spp.; and the grasses Stipa tenuis and Poa ligularis. Foliage cover varies from 35 % to 65 %, but may increase substantially in rainy periods when annual plants contribute a high proportion of the total cover (Beeskow et al. 1995). The Monte Phytogeographic Province is characterised by an open tall shrubland covering 40-60% of the soil surface (Ares et al. 1990). The canopy is formed by an upper layer (1.5 - 2m) dominated by Larrea divaricata, Condalia microphylla, Schynus johnstonii and Chuquiraga hystrix; an intermediate shrubby layer (0.5 - 0.8 m) dominated by Chuquiraga avellanedae; and a lower layer (0.1 - 0.5m), rich in perennial bunchgrasses, dominated by Stipa tenuis and Poa ligularis.

The NE region is a plateau at 60 – 80 m above the sea level (masl), with low-lands of small extension within gentle sloped piedemont sediments. The SE region is a plateau with low, up to 200 m high, rounded rocky hills of volcanic origin that becomes uneven at the coastal margins. The Central region is a high, 600 – 700 masl basaltic plateau, intersected by deep (up to 100 m) canyons.

2.1.3 Description of sites and management conditions

Sites within regions were selected based on previous vegetation maps (Bertiller et al. 1980, Beeskow et al. 1987) to reflect habitat heterogeneity at a smaller scale. Sites were private owned ranches (range 3,500 – 28,000 hectares) in which sheep farming for wool production is the exclusive productive activity. The exception was site 5, in the SE, a provincial wildlife reserve (Reserva Cabo Dos Bahías) of 1,200 ha, where sheep farming was terminated in 1973. The reserve has a permanent warden, and tourism is the only human-related activity.

Typically, Patagonian ranches contain from 1 – 4 permanent residents, depending on the size of the ranch and the number of sheep. Sheep graze the native vegetation. Stock densities vary from 0.15 to 0.25 sheep.ha^{-1}. Ranches are divided in paddocks usually larger than 2,500 ha each, divided by 1 m high fences to prevent sheep moving between paddocks, but guanacos are able to jump over the fences. Water for the animals is ensured by wind-driven pumps to artificial waterpoints. Typically, a single permanent waterpoint is common to 3 – 4 paddocks. Temporary water points are naturally formed in low places where rainfall water accumulates.

Management practices are mainly related to reproductive and health aspects of sheep. Lambing occurs during mid-winter (July – August), with the shearing of adult sheep and marking of the new lambs in the spring. Vegetation management is practically non-existent, as movements of sheep are mainly related to the restrictions imposed by weather conditions rather than planned, seasonal stocking rates (Soriano and Paruelo 1990).

2.2 SURVEYS DESIGN

2.2.1 Animal surveys

Ground surveys of guanacos and sheep were conducted from an open pick-up vehicle with two observers standing in the back, following the line transect method (Burnham et al. 1980, Buckland et al. 1993, see section 5.2 for details). Replicate surveys were conducted travelling along internal roads and tracks within sites. Main, public roads were avoided. Survey design was not random. I chose tracks in order to travel across most of the site, also avoiding roads that were close to each other (< 1,000 m) to reduce the risk of double counting. Within each site, direction of travel was the same for all surveys. Survey length ranged from 10-45 km depending on the site. A total of 3,374 km were travelled in 124 surveys (see section 5.2 for further detail of survey distribution).

Total counts of guanacos were made in site 5, the reserve, in order to compare with the estimates obtained using the line transect method. This is possible in the reserve because it is relatively small (1,200 ha) and guanacos are used to people and cars visiting the site. The area was divided in three blocks of approximately 400 ha each, which were searched on foot. A total of seven counts were conducted during January 1997 (3 counts) and September 1998 (4 counts). In the reserve, the estimates obtained using both methodologies were very similar indeed (Table 2.1).

Table 2.1: Mean number of guanacos in site 5 and densities expressed in guanacos.km^{-2} (± S.E.) as obtained by total counts, and densities obtained using the line-transect method (see *Chapter 5*).

	Total counts		***Line transect***
	Number of guanacos	Density	Density
Summer 1996-1997	**453 ± 14**	**37.75 ± 1.17**	**37.82 ± 0.02**
Spring 1997	**398 ± 15**	**33.17 ± 1.25**	**33.64 ± 2.62**

2.2.2 Vegetation surveys

Vegetation composition, in terms of ground cover, was determined based on the line intercept method (Goodall 1952, Mueller-Dombois and Ellenberg 1974). Between six and twelve vegetation plots were sampled within each of the nine sites. Plots were placed at regular intervals (500 – 1,000 m depending on the site), following the pattern of the line transects surveyed for animal counts (see Figure 3.1 in *Chapter 3* as an example). Across all nine sites, 80 vegetation plots were surveyed once per season. Plots were recorded on a map and subsequently located in the field using a portable GPS. From the centre of each plot four randomly oriented, 50 m transects were surveyed. Records were made at 1 m intervals along each transect, using a sward height stick (5 mm diameter) placed vertically in the vegetation. At each point, plant species and status (green or dry) was recorded for all plants hit by the stick, totalling 200 (4 x 50) data-points per plot.

During the first season (summer 1996 - 1997), vegetation components were recorded as grass, shrubs (woody plants higher than 30 cm) and dwarf shrubs. Ground cover of every vegetation type by site was analysed using canonical variates to validate the previously defined sites (see section 3.2 in *Chapter 3*). For the other seasons (spring 1997 and summer 1997 – 1998) vegetation components were recorded at the species level where possible. Plant species were subsequently grouped into functional types based on different life forms and life strategies, following the criteria by Raunkaier 1937, and Kent and Coker 1992 (see details in *Chapter 3*, section 3.2).

Ground cover of plant functional types or species was estimated by plot as the number of hits recorded in a given plant functional type (or species) divided by 200 (4 x 50). Then, ground cover by site by season was estimated using the mean ground cover by plot within site-season. Relative availability of each plant functional type or species was estimated as the number of records on a given plant functional type (or species) divided by the total number of hits on the vegetation (excluding hits on bare soil). Proportion of live plant material was estimated as the number of records of green parts for a given plant functional type or species divided by the number of hits on that plant functional type.

2.2.3 Collection of faecal pellets of guanacos and sheep

Guanaco and sheep faeces were collected during spring 1997 and summer 1997-1998, to study diet composition through microhistological analysis. Faecal pellets were collected in the proximity of the vegetation plots, immediately after surveying each plot. (see section 4.2 in Chapter 4 for a detailed explanation).

2.3 DATA ANALYSIS

All data was analysed using the GENSTAT 5.3 statistical package. Specific procedures summarised in Table 2.2 are described in detail in the appropriate data chapters.

Table 2.2: Summary of variables, associated methodology and analysis procedures used in the study. See the reference to locate each procedure in detail within the thesis.

Variable	**Method / Estimate**	**reference**
Vegetation cover	Line – intercept	*Chapter 3*
Proportion of live material	Line – intercept	
Variation in vegetation composition	General ANOVA	
Between-site similarity in vegetation composition	Canonical Variates analysis Kulcyznski's similarity index	
Plant species richness	Jakknife estimate. T-tests for paired samples between seasons	
Faecal analysis	Microhistological analysis	*Chapter 4*
Diet composition	Frequency of dietary components in faeces	
Between-herbivores and Within-herbivores seasonal differences in proportion of dietary components.	T-tests for paired samples	
Dietary overlap between guanacos and sheep	Kulcyznski's similarity index Randomisation analysis	
Diet similarity between seasons	Kulcyznski's similarity index Randomisation analysis	
Similarity diet-availability in the environment	Kulcyznski's similarity index Randomisation analysis	
Dietary selectivity	Ivlev's Electivity index	
Population densities	Line – transect surveys Distance estimates based on detection function	*Chapter 5*
Spatial and temporal variation in guanaco densities	Generalised linear models / Analysis of deviance	

Chapter 3. SPATIAL AND SEASONAL VARIATION IN VEGETATION COMPOSITION

3.1 INTRODUCTION

The change from semi-arid to arid conditions has been associated with changes in the vegetation from dominant herbaceous plants (grasses and forbs) to woody plants (shrubs) (Reynolds et al. 1997). Grasses often dominate the steppe regions (Fischer and Turner 1978) accounting for up to two thirds of the primary productivity in arid and semi-arid lands (Fernández et al. 1991). In addition to spatial variation in the abundance of different plant life forms, plants have developed different life strategies in an environment in which rainfall is largely unpredictable and highly variable between years (Noy-Meyr 1973). While evergreen shrubs are deeply rooted and adapted to use the water available in the lower layers of the soil, other life forms like deciduous shrubs and herbs are closely dependent on water inputs and therefore restricted to developing in periods when water and nutrients are available in the upper soil (Fischer and Turner 1978, Sala et al. 1989). Consequently, herbaceous and some woody-deciduous perennials show pulses of assimilation closely related to short-term rainfall, while woody evergreen perennials maintain green tissues during the entire year, including the dry summer season. During periods of water stress, reproduction of grasses and forbs may be interrupted shortly after initiation or even may not start (Bertiller et al. 1991).

Two main physiognomies generally characterise the vegetation of arid and semi-arid Patagonia as herbaceous and shrub steppes (Beeskow et al. 1995). Vegetation structure is patchy, with different shrub layers and tussock-grasses overlapped forming high-cover spots surrounded by areas with isolated grasses and a high proportion of bare soil (Bertiller et al. 1991, Aguiar and Sala 1999). As described in the previous chapter (see section 2.1.2), the Central region in my study area belongs to the Monte Phytogeographical Province and it is located in the arid zone, whilst the NE and SE regions are included in the Patagonian Phytogeographical Province, in the semi-arid zone (Soriano 1956).

On the basis of these gross differences in physiognomies between regions I expect substantial variation in the relative abundance of plant life forms in space and time which in turn will influence the availability of different food types for the foraging herbivores. My aim in this chapter is to describe the vegetation composition of the study area at both regional and local site scales, as well as seasonal changes. I will analyse the variation in vegetation composition in space and time in terms of plant functional types and describe the plant species composition within types.

3.2 MATERIALS AND METHODS

Vegetation surveys

Vegetation composition, in terms of ground cover, was determined based on the line intercept method (Goodall 1952, Mueller-Dombois and Ellenberg 1974). Between six and twelve vegetation plots were sampled within each of the nine sites. Plots were placed at regular intervals (500 – 1,000 m depending on the site), following the pattern of the line transects surveyed for animal counts (see Figure 3.1 as an example).

Figure 3.1: Distribution of vegetation plots (●) at site 6. Lines are tracks used for animal survey transects. Distances are in km.

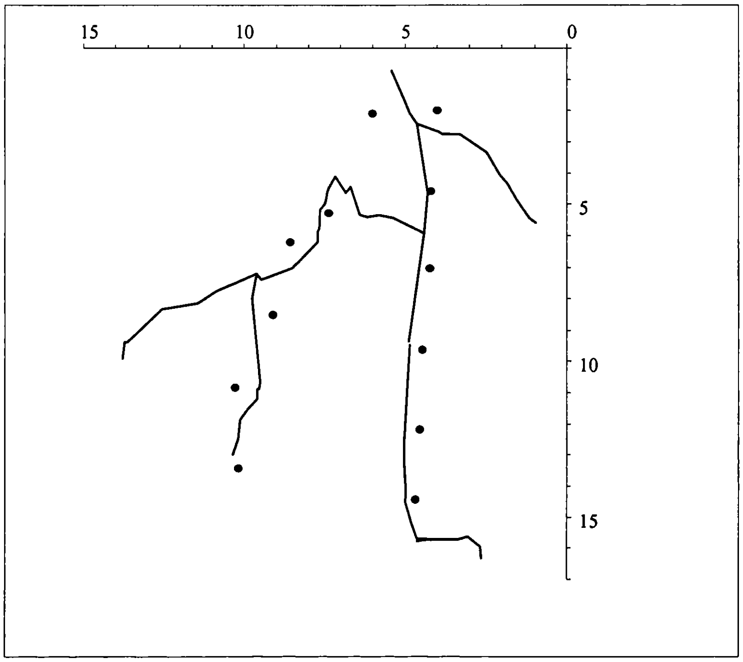


Table 3.1: Number of vegetation plots surveyed by site by season

Site	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Number of plots	6	6	12	8	12	12	12	6	6

Across all sites there were a total of 80 plots (Table 3.1), and all plots were surveyed once per season. Plots were relocated each season using a portable GPS. From the centre of each plot four randomly oriented, 50 m transects were surveyed. Records were made at 1 m intervals using a graduated stick (5 mm diameter) placed vertically in the vegetation. At each point, plant species and status (green or dry) was recorded for all plants hit by the stick, totalling 200 (50 x 4) data-points per plot. This method may overestimate plant cover but gives a good estimate of the relative proportions of different plant types and species (Goodall 1952). During the first season (summer 1996-

97), I recorded only the following plant types: shrubs (woody plants higher than 30 cm height), dwarf shrubs (woody plants lower than 30 cm height), and grasses. Also, the most common species were recorded within each category. For the other seasons (spring 1997 and summer 1997-98), I recorded plant species. Unknown species were provisionally identified with a number and subsequently taken to the Museo de Ciencias Naturales de Puerto Madryn for proper identification by technicians. Identification was made at species level when possible, otherwise the genera level was used. The main reference source used for plant identification was Flora Patagonica (Correa 1984).

Data analysis

Results in this chapter are based on the vegetation data obtained during spring 1997 and summer 1997-98. I used data obtained during the first season (summer 1996-97) to validate the assumption that within site variation in vegetation composition was smaller than between sites, within regions. Relationships among groups of plots in terms of proportions of all three plant types defined in the first season were assessed through canonical variates analysis (CVA). Depending on the site, two groups of 4-6 plots were combined for CVA. For each combination, the following three variables were defined: (1) proportion of shrubs; (2) proportion of dwarf shrubs and (3) proportion of grasses. Plot discrimination by canonical variate analysis was consistent with that originally distinguished from published maps. Groups of plots within the same site were in general more similar than groups of plots from other sites within the same geographical region (Table 3.2).

Table 3.2: Inter-group distances estimates by canonical variate analysis. As an example, groups of plots A and B belong to site 1 in the NE region, and groups C and D are in site 2. Distance between A and B is 1.45 and distance between C and D is 1.95. Both distances are smaller than distances between groups of plots from different sites within the same region (i.e. compare with A-D: 2.91 or B-C: 3.17 or B-D: 3.88).

Region	Site	Group	Distances														
NE	1	A	0.00														
	1	B	1.45	0.00													
	2	C	2.01	3.17	0.00												
	2	D	2.91	3.88	1.95	0.00											
	3	E	2.12	3.30	1.24	0.95	0.00										
	3	F	2.23	2.74	2.14	1.43	1.52	0.00									
	4	G	6.44	5.74	6.28	6.56	6.70	5.59	0.00								
SE	5	H	2.88	3.73	1.86	3.79	3.09	3.79	6.41	0.00							
	5	I	3.63	4.11	2.68	4.44	3.90	4.25	5.58	1.24	0.00						
	6	J	3.73	3.95	2.66	3.53	3.44	3.13	3.95	2.76	2.21	0.00					
	6	K	3.52	3.87	2.34	3.34	3.19	3.04	4.33	2.41	1.95	0.38	0.00				
	7	L	2.30	3.17	0.93	2.74	2.14	2.65	5.77	1.18	1.76	2.05	1.70	0.00			
	7	M	2.04	3.16	0.14	2.06	1.38	2.21	6.20	1.74	2.54	2.55	2.22	0.79	0.00		
C	8	N	3.22	1.86	5.00	5.42	4.98	4.12	6.07	5.52	5.75	5.43	5.43	5.00	5.00	0.00	
	9	O	4.83	3.39	6.31	6.92	6.54	5.55	5.33	6.41	6.25	5.88	5.99	6.02	6.26	2.11	0.00
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O

Plant species were grouped into seven different plant functional types (Table 3.3) according to different life forms and strategies (Raunkaier 1937, Kent and Coker 1992). Plant ground-cover per plot was estimated as the number of hits for a plant functional type or species divided by the total number of points in the plot (200 points). Availability of plant functional types or species was estimated by dividing the number of hits on a particular functional type or species by the total number of hits on the vegetation. Differences between regions, sites and seasons for every plant functional type were analysed using general ANOVA models, including contrasts between regions. Angular transformation of proportions was applied for statistical analysis on seasonal, regional and local variation.

Table 3.3: Plant functional types used to categorise plant species in sample sites during spring 1997 and summer 1997-98.

Dicotyledoneous plants

1. PHANEROPHYTES: woody dicotyledoneous plants > 30 cm height
1.1 Evergreen phanerophytes
1.2 Deciduous phanerophytes

2. CHAMAEPHYTES: woody dicotyledoneous plants < 30 cm height
2.1 Evergreen chamaephytes

3. FORBS: non-woody dicotyledoneous plants
3.1 Perennial forbs
3.2 Annual forbs

Monocotyledoneous plants

4.1 Perennial grasses
4.2 Annual grasses

Species richness was estimated using the Jackknife procedure, recommended when the estimate is based in the number of species occurring in plots or quadrats (Krebs 1989). Seasonal differences in species richness were investigated using t-tests for paired samples.

$$\boldsymbol{S} = \mathbf{s} + (\mathbf{n} - \mathbf{1} \; / \; \mathbf{n})^{k}$$

where:

S: Jackknife estimate of species richness
s: Observed total number of species present in *n* plots
n: Total number of plots sampled
k: number of unique species

3.3 RESULTS

3.3.1 Vegetation composition: plant functional types

Spatial variation in ground cover

There were significant differences in ground cover of all plant functional types between regions and between sites (Figure 3.2, Table 3.4) With the exception of evergreen phanerophytes, regional effects accounted for more of the variation in vegetation cover in space than site effects (see Appendix 1). The Central region had the highest cover of deciduous phanerophytes and chamaephytes (Figure 3.2), and the lowest cover of evergreen phanerophytes (due to the low cover in site 8, see Figure 3.3), perennial grasses and forbs. Also, the total ground cover was lowest in the Central region than in the North East and South East (Table 3.4). The last two regions did not differ in the cover of phanerophytes and chamaephytes, but the NE had a higher cover of perennial grasses, perennial forbs and annual forbs than the SE, while the ground cover of annual grasses was significantly higher in the SE than in the NE (see Table 3.4 and Appendix 1).

Although regional effects were dominant, site effects were significant for all plant functional types, especially for evergreen phanerophytes (Table 3.4, Appendix 1). Site effects were important for perennial grasses (Table 3.4, Appendix 1) largely because of the high cover of perennial grasses estimated in site 4 (Figure 3.3).

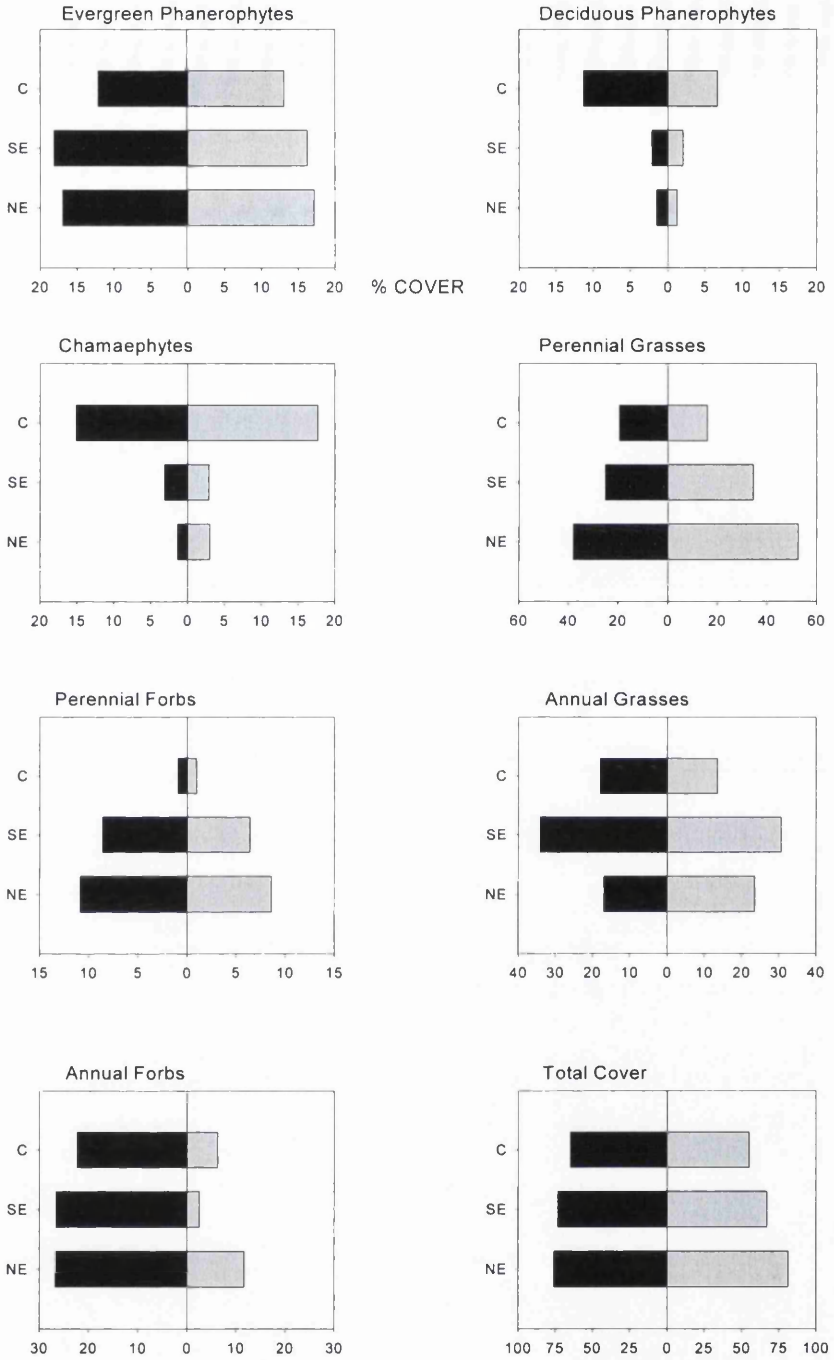


Figure 3.2: Percent ground cover of plant functional types by region by season (C: central, SE: South East, NE: North East; ■ Spring 1997, ▨ Summer 1997-98). Number of plots per season: *NE=32, SE=36, C=12*

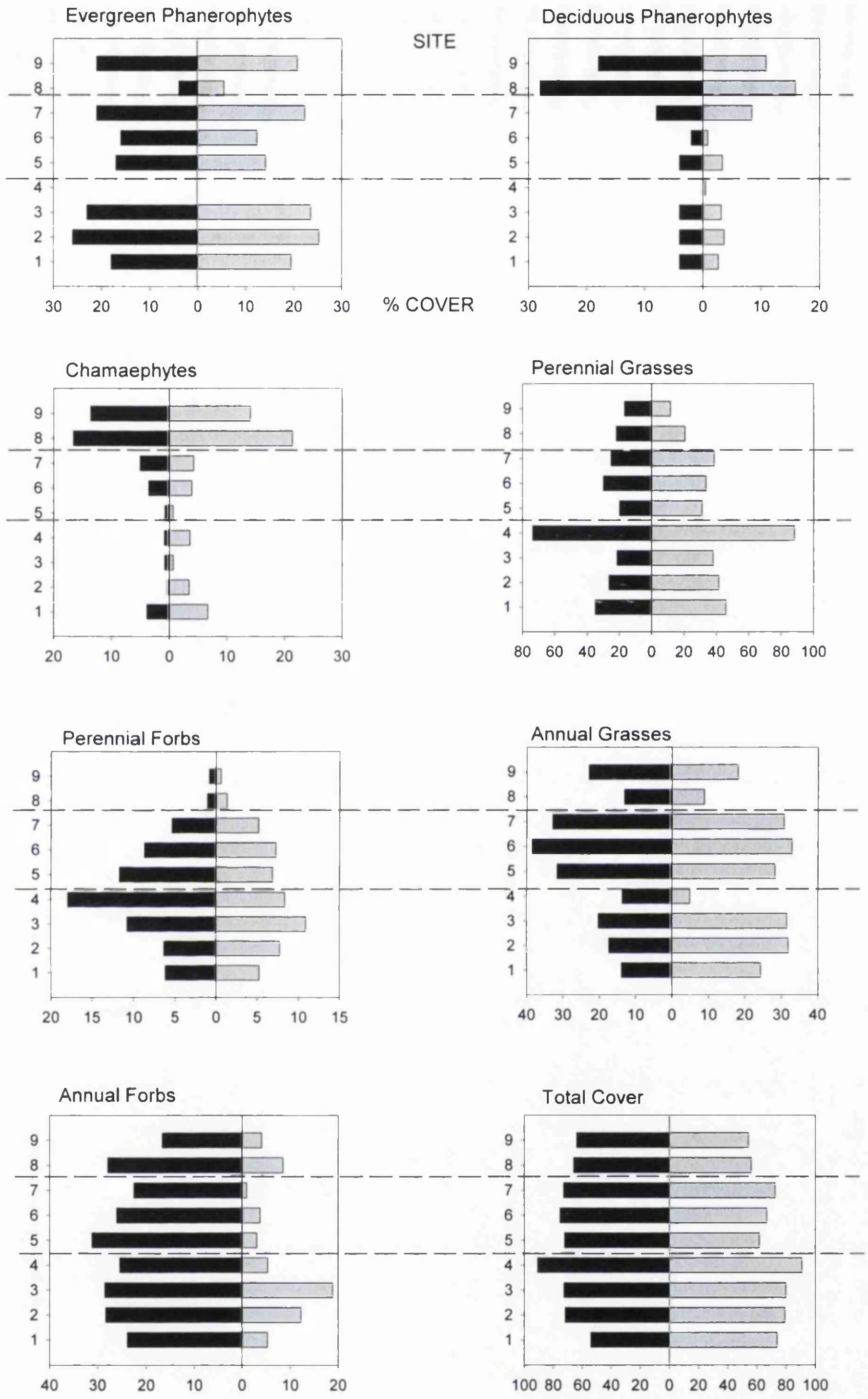


Figure 3.3: Percent ground cover of plant functional types by site by season (■ Spring 1997, ■ Summer 1997-98). Sites 1 to 4 are in the NE region, 5 to 7 in the SE and sites 8 and 9 in the Central region.

Table 3.4: Spatial variation in vegetation cover: statistical significance of ANOVA tests for the different plant functional types and total ground cover across Region and Sites, including orthogonal contrasts between regions (*rest*: two regions combined to test for differences against the third, *N.S.*: non significant). See *Appendix 1* for the general ANOVA models.

Plant Functional Type		Between Regions d.f. = 2	Contrasts between Regions d.f. = 1	Between Sites d.f. = 6
Evergreen Phanerophytes	***F*** ***p***	4.05 (<0.05)	*C < rest* 4.11 (0.045) *NE < SE* 3.99 (0.048)	46.25 (<0.001)
Deciduous Phanerophytes	***F*** ***p***	50.26 (<0.001)	*C > rest* 99.27 (p<0.001) *NE = SE* 1.27 (N.S.)	9.47 (<0.001)
Chamaephytes	***F*** ***p***	61.18 (<0.001)	*C > rest* 122.4 (p<0.001) *NE = SE* 0.00 (N.S.)	3.27 (<0.01)
Perennial Grasses	***F*** ***p***	50.40 (<0.001)	*NE > rest* 85.00 (p<0.001) *SE > C* 15.80 (p<0.001)	31.84 (<0.001)
Perennial Forbs	***F*** ***p***	61.69 (<0.001)	*C < rest* 117.99 (p<0.001) *NE > SE* 5.39 (p<0.05)	5.91 (<0.001)
Annual Grasses	***F*** ***p***	21.62 (<0.001)	*SE > rest* 42.16 (p<0.001) *NE = C* 1.09 (N.S.)	5.21 (<0.001)
Annual Forbs	***F*** ***p***	10.03 (<0.001)	*SE < rest* 14.11 (p<0.001) *C < NE* 5.94 (p<0.05)	4.63 (<0.001)
Total Cover	***F*** ***p***	22.79 (<0.001)	*C < rest* 27.88 (p<0.001) *NE > SE* 17.69 (p<0.001)	5.67 (<0.001)

Availability and similarity of plant functional types between sites

Across sites, perennial grasses made up between 15 and 50 % of the total cover in spring, and from 15 to 90 % in summer (Figure 3.4). Chamaephytes made the smallest contribution, although their relative proportion was more important in summer due to the reduction in the availability of perennial and annual forbs. Sites 1, 2 and 3 in the NE region and sites 5, 6 and 7 in the SE had a high availability of evergreen phanerophytes but a low availability of deciduous phanerophytes and chamaephytes. These two last functional types were more important in sites 8 and 9 in the Central region while perennial forbs availability was low. In contrast, site 4 in the NE also had the highest availability of perennial grasses and perennial forbs and lowest of phanerophytic shrubs (<1%). Sites 5, 6 and 7 in the SE had the highest proportion of annual grass available, while site 4 in the NE had the lowest (Figure 3.4).

Figure 3.4: Contribution of each plant functional type to total plant cover by site (availability). Sites 1 to 4 are in the NE region, 5 to 7 in the SE and sites 8 and 9 in the Central region.

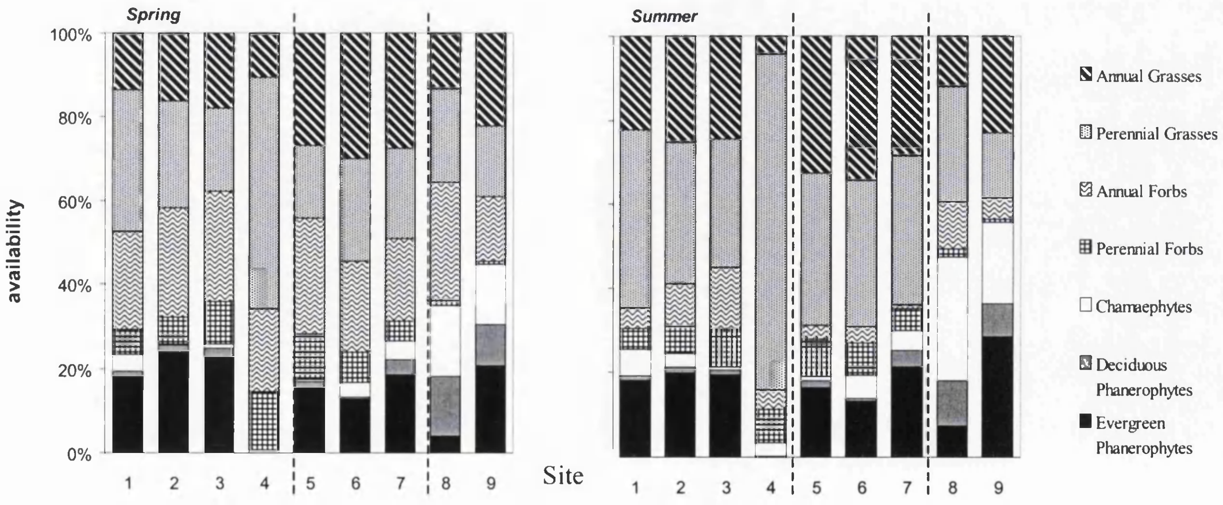


Table 3.5: Similarity between sites in terms of availability of plant functional types in spring and summer. Values are percentages (Kulzynski's Similarity Index).

	Spring										*Summer*								
Site	1	2	3	4	5	6	7	8	9		1	2	3	4	5	6	7	8	9
1	100										100								
2	87	100								*NE*	88	100							
3	83	92	100								82	92	100						
4	70	61	60	100							60	52	48	100					
5	78	83	90	57	100						86	88	85	53	100				
6	81	82	81	61	87	100				*SE*	84	85	81	55	94	100			
7	82	82	84	56	86	90	100				88	90	82	50	90	88	100		
8	69	69	68	53	65	65	67	100			61	63	62	42	55	57	58	100	
9	71	73	77	45	74	73	83	74	100	*C*	69	71	67	29	63	62	71	67	100

Similarity in terms of percentage of different functional types available tended to be highest between sites within the same region (Table 3.5), although with some exceptions. In the NE region, similarity between sites 1, 2 and 3 ranged from 83 to 92 %. These sites were more similar to sites 5, 6 and 7 in the SE than to site 4. Similarity between site 4 and the rest of the sites in the NE ranged from 60 to 70 % in spring and from 48 to 60 % in summer (Table 3.5). In the Central region, similarity between sites 8 and 9 varied between 67 and 74 % depending on the season.

Seasonal variation in ground cover and interaction effects

Seasonal differences in vegetation cover were significant for some of the herbaceous plant types but not for woody dicots (Table 3.6). Ground cover of perennial grasses was significantly higher in summer than in spring, while both perennial and annual forb cover was lower in summer (Table 3.6). Only seasonal variation in annual forb cover accounted for more variation than spatial, regional or site effects (Appendix 1). There were significant interaction effects between regions and seasons in perennial grass cover (Table 3.6) because it was higher in summer for the NE and SE than in

Table 3.6: Seasonal variation in plant cover and interactions (*Region by Season* and *Site by Season*). Statistical significance of ANOVA tests for (1) the different plant functional types and total ground cover between seasons, and (2) Region by Season and Site by Season interactions, including orthogonal contrasts between regions by season (*rest*: two regions combined to test for differences against the third, *N.S.*: non significant, significant effects are shown in *bold* type). See *Appendix 1* for the general ANOVA models.

Plant Functional Type		Between Seasons d.f. = 1	Region by Season Interaction d.f. = 2	Contrasts between Region by Season d.f. = 1	Site by Season Interaction d.f. = 6
Evergreen Phanerophytes	*F* *P*	0.37 (N.S.)	0.71 (N.S.)	*C = rest* 0.58 (N.S.) *NE = SE* 0.83 (N.S.)	0.23 (N.S.)
Deciduous Phanerophytes	*F* *p*	2.30 (N.S.)	1.99 (N.S.)	*C = rest* 3.62 (N.S.) *NE = SE* 0.36 (N.S.)	0.36 (N.S.)
Chamaephytes	*F* *p*	0.52 (N.S.)	0.69 (N.S.)	*C = rest* 0.25 (N.S.) *NE = SE* 1.13 (N.S.)	0.44 (N.S.)
Perennial Grasses	*F* *p*	**19.34** **(<0.001)**	**4.18** **(<0.05)**	*NE = rest* 3.82 (N.S.) *C ≠ SE* **4.54 (<0.05)**	0.45 (N.S.)
Perennial Forbs	*F* *p*	**5.63** **(p<0.05)**	0.57 (N.S.)	*C = rest* 0.96 (N.S.) *NE = SE* 0.17 (N.S.)	**2.60** **(<0.05)**
Annual Grasses	*F* *p*	0.04 (N.S.)	2.97 (N.S.)	*SE = rest* 2.51 (N.S.) *NE = C* 3.42 (N.S.)	1.16 (N.S.)
Annual Forbs	*F* *p*	**239.37** **(<0.001)**	**8.04** **(<0.001)**	*SE ≠ rest* **18.08 (p<0.001)** *C = NE* 0.09 (N.S.)	1.38 (N.S.)
Total Cover	*F* *p*	0.81 (N.S.)	**5.05** **(<0.01)**	*C = rest* 2.35 (N.S.) *NE ≠ SE* **7.75 (p<0.01)**	0.58 (N.S.)

spring, while in the Central region was lower in summer (Figure 3.2). Also, the interaction between regions and seasons was as it was lowest in the Central region in spring but in summer the lowest cover was estimated in the SE (Figure 3.2). Region by season interaction for total cover was significant due to differences between the NE and SE (Table 3.6, Figure 3.2). There was a significant site by season interaction in perennial forbs cover (Table 3.6).

3.3.2 Vegetation composition: plant species

Regional composition

A total of 102 different plant species making up 79 genera and 38 families were identified across all regions (Appendix 2). I found 37 species of woody dicotyledoneous plants (11 evergreen phanerophytes, 12 deciduous and 14 chamaephytes), 18 species of grasses and graminoids (11 perennial grasses and 5 annual grasses) and 47 species of forbs (23 perennial and 24 annual forbs). From the 102 plant species, 76 (74.5 %) were found in the North East region, 68 (66.7 %) in the South East and 62 (60.8 %) in the Central region.

The dominant plant species in North East and South East regions were the phanerophytes Chuquiraga avellanedae and Lycium chilense, the chamaephytes Mulinum Spinosum and Nassauvia spp. and the perennial grasses Stipa tenuis and Poa ligularis. In the Central region, dominant species were the phanerophytes Larrea divaricata, Condalia microphylla, Schynus johnstonii and Chuquiraga hystrix and the perennial grasses Stipa tenuis and Poa ligularis.

Local site composition and similarity

In sites 1, 2 and 3 the shrubby layer was dominated by Chuquiraga avellanedae in sites representing around 20 % of the plants available (Table 3.7). Other phanerophytes, available in smaller proportions, were the evergreen Schinus johnstonii, and the deciduous Lycium chilense and Prosopidastrum globosum. The dwarf-shrub layer (chamaephytes) was dominated by Nassauvia ulicina and Mulinum spinosum. The herbaceous layer was dominated by perennial grasses of the genus *Stipa* representing between 27 and 34 % of the plants available, with Stipa tenuis as the dominant species. Also, availability of the perennial grass Poa ligularis was important (around 7 %). The most common annual grasses were Schismus barbatus and Vulpia spp., while the forb Erodium cicutarium represented 11 % of the plants available during spring. Phanerophytes availability was lower than 1 % in site 4, while the availability of the perennial grass Stipa tenuis was 60 %. Chuquiraga avellanedae was also the dominant evergreen shrub in sites 5, 6 and 7 in the SE, where Colliguaya integerrima was common. Nassauvia ulicina and Chuquiraga aurea dominated the dwarf-shrub layer, while the grasses Stipa spp. were dominant in the herbaceous layer, together with the annual grass Vulpia spp. In the Central region, the deciduous shrub Prosopis denudans was dominant in site 8 while the evergreen Larrea spp. was dominant in site 9. The dwarf shrub layer was dominated by Acantholippia seriphioides, while several species of the perennial grass *Stipa* were common in the herbaceous layer.

Table 3.7: Main plant species by site and percentage available in relation to total cover. Dominant species in each group are shown in bold type. Species without percent value represented less than 1 % of total plant cover. Herbaceous layer includes perennial and annual grasses and forbs. [(sp) = spring season].

Site	Phanerophytes	Chamaephytes	Herbaceous layer
1	***Chuquiraga avellanedae*** 18% *Lycium chilense* *Prosopidastrum globosum*	***Nassauvia ulicina*** 4% *Accantholippia seriphioides* *Chuquiraga erinacea*	***Stipa tenuis, Poa spp.*** 37 % *Schismus barbatus* 13 % *Erodium cicutarium* 11% (sp) *Plantago patagonica* 5%
2	***Chuquiraga avellanedae,*** ***Chuquiraga hystrix*** 20% *Schinus johnstonii* 3% *Junellia spp.*	***Mulinum spinosum*** 3% *Accantholippia seriphioides*	***S. tenuis, S. speciosa,*** ***Poa spp*** 30 % *S. barbatus, Vulpia spp.* 20 % Important forbs as in site 1
3	***Chuquiraga avellanedae*** 20% *Lycium spp.* *Condalia microphylla.* *P. globosum*	*Accantholippia seriphioides* *Baccharis spp.*	***S. tenuis, S. speciosa, S. neaei,*** ***Poa spp.*** 24 % *S. barbatus, Vulpia spp.* 17 % Important forbs as in sites 1,2
4	*Junellia spp.* *Ephedra ochreata*	***Mulinum spinosum*** 3%	***S. tenuis*** 60% ***Poa spp.*** 13% *Distichlis spp.* *Vulpia spp.* 9% (sp) *E. cicutarium* 8 % (sp) *Facelis retusa* 3% (sp) *Plantago patagonica* 3%
5	***Chuquiraga avellanedae*** 18% *Colliguaya integerrima* *Lycium spp.*	*Mulinum spinosum* *Frankenia patagonica* *Chuquiraga aurea*	***S. tenuis*** 13% ***Hordeum spp.*** 9% ***S. barbatus*** 6%,***Vulpia spp.*** 20% *Bromus spp.* 4% *Herniaria cinerea* 7% *E. cicutarium* 21% (sp)
6	***Chuquiraga avellanedae*** 7% *Colliguaya integerrima* 6%	***Nassauvia ulicina*** 2% *Chuquiraga aurea*	***S. tenuis, S. pampeana*** 15% ***Vulpia spp.*** 23% *Hordeum spp.* 4% *E. cicutarium* 11% (sp)
7	***Chuquiraga avellanedae*** 10% *Colliguaya integerrima* 7% *Prosopidastrum globosum* 1% *Lycium spp.* *Schinus johnstonii*	***Chuquiraga aurea*** 3%	***S. tenuis, S. pampeana,*** ***S. longilumilis*** 15% ***Vulpia spp.*** 21% *Poa spp.* 5% *E. cicutarium* 8% (sp)
8	***Prosopis denudans*** 6% *Schinus johnstonii* 2% *Larrea spp.* 2 % *Lycium spp.*	***A. seriphioides*** 9% *Junellia seriphioides* 6% *Mulinum spinosum* 4%	***S. chrisophylla, S. tenuis*** 17% *Schismus sp. 9%* *Poa spp.* 5% *Plantago patagonica* 10%
9	***Larrea spp.*** 10% *Schinus johnstonii* 5% *Chuquiraga hystrix* 5% *Lycium spp.* 2% *Prosopis spp.* 2%	***A. seriphioides*** 12%	***S. pampeana, S.chrisophylla,*** ***S. tenuis*** 11% ***Schismus sp.*** 21% *Plantago patagonica* 8%

Table 3.8: Similarity between sites in terms of availability of dominant plant species (18 spp.) in spring and summer. Values are percentages (Kulzynski's Similarity Index).

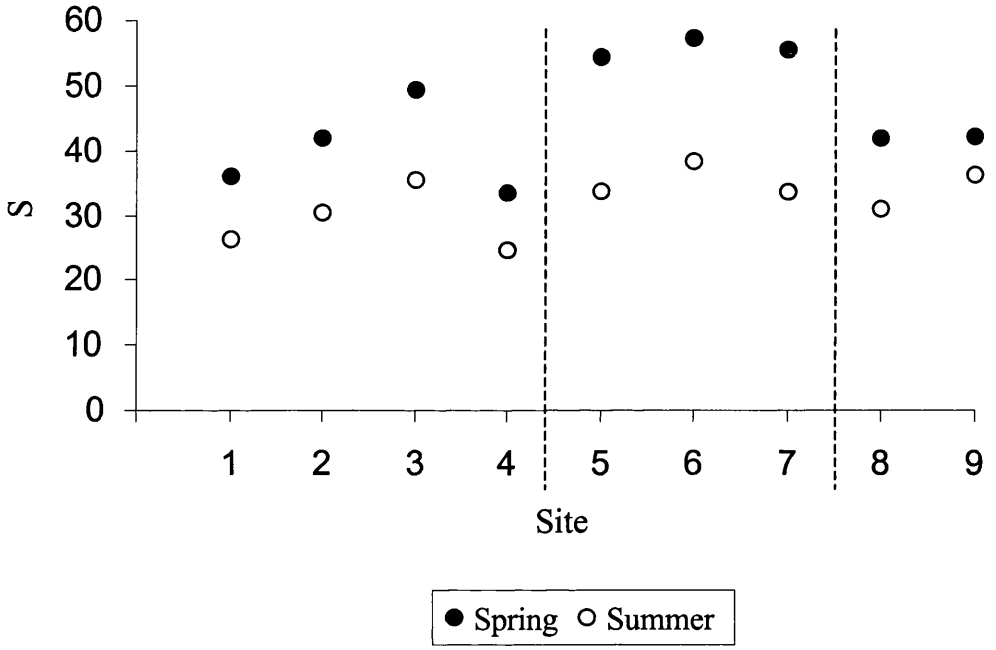
	Spring										***Summer***								
Site	1	2	3	4	5	6	7	8	9		1	2	3	4	5	6	7	8	9
1	100										100								
2	80	100								*NE*	85	100							
3	79	94	100								85	89	100						
4	61	49	48	100							49	43	38	100					
5	61	65	65	43	100						70	69	73	40	100				
6	57	57	54	52	70	100				*SE*	65	59	62	43	79	100			
7	59	64	64	49	71	83	100				67	67	68	41	75	83	100		
8	48	55	55	34	37	33	40	100			52	60	59	37	35	36	40	100	
9	48	57	57	31	36	33	38	60	100	*C*	49	55	49	20	31	29	36	58	100

Similarity between sites in the proportion of the dominant plant species available (Table 3.8) followed a similar pattern than for plant functional types. Sites within region were in general more similar than sites in different regions, again with the exception of site 4 in the NE. Unlike for plant functional types, sites 1, 2 and 3 in the NE were more similar among them (79 – 85 %) than to sites 5, 6 and 7 (57 – 63 %) in the SE. Similarity between the SE sites (5, 6 and 7) ranged between 70 – 83 %, and from 58 – 60 % between sites 8 and 9 in the Central region. Similarities between these sites and the rest of the sites were substantially lower (Table 3.8), in accordance with the pattern found for plant functional types (Table 3.7).

Plant species richness

Number of plant species (species richness) estimated for each site ranged from 33 in site 4 to 57 in site 6 during spring, but from only 25 to 31 species in the same sites during the summer (Figure 3.5). Mean species richness in spring (45.8) was significantly higher than in summer (32.2 species); ($t = 7.28$, $p < 0.001$, d.f. = 8), mainly due to a decrease in the number of species of annual forbs from 10 - 15 species in spring to 1-8 species in summer depending on the site.

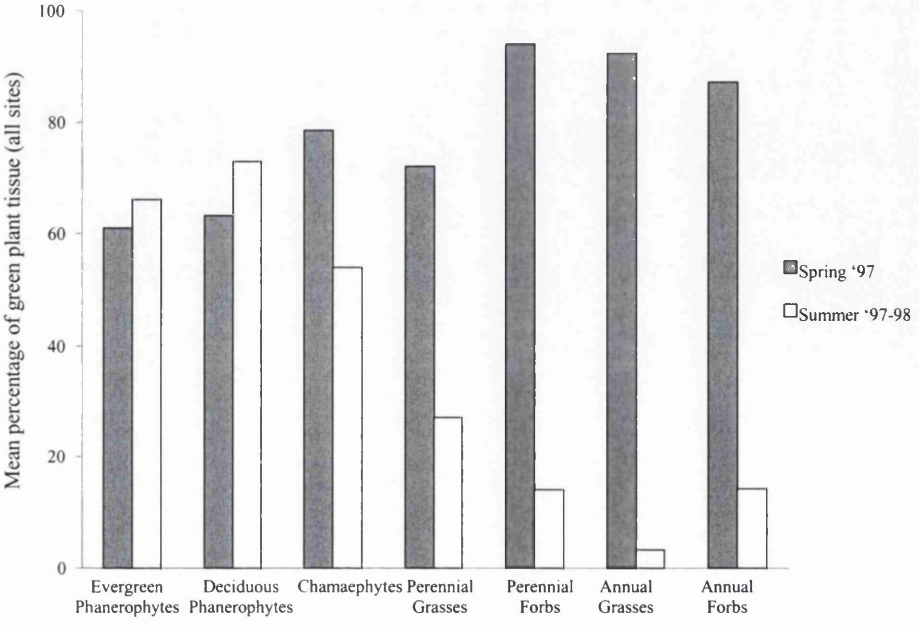
Figure 3.5: Species richness (S, Jackknife estimate) by site and season (spring 1997 and summer '97-98). Richness is expressed as the number of plant species (sites 1 to 4 are in the NE region, 5 to 7 in the SE and sites 8 and 9 in the Central region).



3.3.3 Proportion of live plant material

The percentage of live plant tissue, in terms of proportion green, was significantly lower in summer than in spring for all the functional types forming the herbaceous layer (Figure 3.6, d.f. = 8 in all cases). While 72 % of perennial grass tissue was green in spring, only 27 % remained green in summer ($t = 5.11$, $p < 0.001$). The proportion of perennial forbs green declined from 94 to 14 % ($t = 13.65$, $p < 0.001$), while 92 % of annual grass material was green during spring and only 3 % in summer ($t = 29.16$, $p < 0.001$). Proportion of annual forbs green material decreased from 87 % in spring to 14 % in summer ($t = 20.72$, $p < 0.001$). Among the woody dicots, percentage of green tissue of evergreen phanerophytes was higher in summer than in spring (66 vs. 61 %, $t = -2.57$, $p < 0.05$) while for chamaephytes it was lower in the summer ($t = 2.40$, $p < 0.05$).

Figure 3.6: Mean percentage of green tissue by plant functional type by season.



3.4 DISCUSSION

Spatial variation in vegetation composition

Although ground cover of plant functional types varied across regions and sites, regional differences generally accounted for more of the spatial variation than local, site effects. The major differences in terms of proportions of shrubs and herbs (grasses plus forbs) were between the Central and the two other regions combined (NE and SE). Ground cover of woody plants was around 40 % in the Central region, whereas the estimates for the NE and SE were around 18 and 23 %. This agrees with the increasing trend in proportion of shrubs as the habitat changes from semi-arid to arid conditions (Reynolds et al. 1997, see also section 2.1.1). As annual rainfall increased from 125 mm in the Central region to 225 – 250 mm in the other regions, grass cover increased from 30 % in the arid Central region up to 65 –75 % in the semi-arid SE and NE during the summer (Figure 3.2). Between site variation was generally consistent with regional variation in ground cover (Figure 3.3), with the exception of evergreen phanerophytes and perennial grass. This was due to site 4 in the NE, having the lowest cover of evergreen shrubs and the highest of perennial grasses, and site 8 in the Central region having a very low cover of evergreen shrubs.

Plant species composition varied regionally in terms of dominant evergreen shrubs. While Chuquiraga avellanedae was the dominant species in the NE and SE, Larrea spp. dominated the Central region. The former shrub has strong spines which would act as structural defence against herbivores (Crawley 1983) although its leaves are palatable (Somlo et al. 1997) while Larrea spp. has no structural deterrent but a high proportion of tannins in the leaves which makes it unpalatable (Raveta and Soriano

1998). Perennial grasses of the genus *Stipa* were dominant in all sites, often with Poa spp. in the NE and with Hordeum spp. in the SE sites. In fact, Stipa and Poa can account for up to 98 % of the above-ground biomass of grasses and forbs (Soriano et al. 1976). Ground cover of the dominant perennial grasses varied between 73 % in site 4 and only 11 % in site 9. Differences in ground cover between plant types are expected to be related to differences in aboveground net primary production (ANPP) as this is a function of the leaf area (Crawley 1983). In SW Chubut, grasses, shrubs and forbs account for 64, 33 and 3 % of the canopy cover and 53, 43 and 4 % of the ANPP respectively (Fernández et al. 1991).

Seasonal variation in vegetation composition

Significant variation in ground cover between seasons was observed for plant types in the herbaceous stratum only. Perennial grass cover was higher in summer than in spring, possibly due to the development of flowerstems and flowers in late spring, persisting during the summer. Perennial and annual forb cover was substantially lower in summer than in spring. The reduction in ground cover for perennial and annual forbs from spring to summer is consistent with their life strategies, closely related to water inputs which are more frequent in late winter and spring. The general, seasonal differences between shrubs and herbs agree with the observed asynchrony in the phenology of different species in the area (Bertiller et al. 1991). Although perennial and annual grasses ground cover did not decreased significantly from spring to summer, the reduction in the proportion remaining green was highly significant (Figure 3.6). Also, the proportions of perennial and annual forbs that were live declined substantially as the dry, summer season progressed. In contrast, the percentage of evergreen phanerophytes that was live increased during the summer (Figure 3.6). Although there was an increase in the average proportion of live tissue for deciduous shrubs, it was not significantly different between spring and summer. The reason may be the different life strategies of deciduous shrub species. While Lycium spp. and Cyclolepis genistioides develop their leaves in late winter, other deciduous like Prosopidastrum globosum and Prosopis spp. do so in summer (Bertiller et al. 1991) increasing their nutritive value (Somlo et al. 1985). In addition to the effect on ground cover and proportion of live plant material, there was a significant reduction in species richness by site from spring to summer. This was mainly due to the decline in the proportion of the ephemeral, annual forbs.

In summary, the abundance and relative proportions of woody and herbaceous plants in the Patagonian steppe varied in space and time. Spatial variation occurred particularly at the regional scale defined in this study. The Central region, with the lowest grass cover, had the highest ground cover of shrubs. Seasonal variation from spring to summer resulted in the reduction of perennial and annual forb cover, together with a significant decrease in the number of species. Also, all the functional types composing the herbaceous layer showed significantly lower proportions of live plant material as spring progressed into summer. This strongly suggest that forage resources for the herbivores are more limited in summer than during spring. In the following chapter, I will assess the feeding strategies of both guanacos and sheep by studying the variation in diet composition and selection in relation to the spatial and seasonal variation in vegetation composition.

Chapter 4. THE FEEDING STRATEGIES OF GUANACOS AND SHEEP

4.1 INTRODUCTION

Ungulate species have been classified as grazers, browsers or intermediate feeders depending on their feeding strategy and on comparative anatomical evidence (Hofmann and Stewart 1972). Browsers have digestive systems adapted to minimise the passage time of ingesta in order to obtain the energy readily available in dicotyledoneous plant tissues. Morphological adaptations in browsers, compared to grazers, include a relatively small reticulorumen, reduced rumen papillation and a high motility digestive system (Hofmann 1973, 1989, see section 1.2). In contrast, the digestive system of grazers is adapted to slow down the passage of ingesta and therefore to obtain energy from a low-quality diet, while intermediate feeders were described as having seasonal morphological changes in rumen papillation, related to variation in the diet (Hofmann 1973, 1989).

Jarman (1974) proposed an alternative explanation to account for the diversity of ungulate feeding strategies. In a classic study of the ecology of African antelope, he assigned feeding categories to different species based on the dispersion and availability of forage species (monocotyledoneous and dicotyledoneous plants) in the environment (see section 1.2). Jarman found a general relationship between body size and feeding style, with the animals below 50 kg body weight tending to be more selective (browsers) than larger ones (grazers, above 200 kg) suggesting that small animals need high quality food because their energetic requirements are relatively high compared to large animals.

In addition, it has been suggested that browsers show morphologic adaptations favouring selective feeding strategies, including a narrow incisor arcade that allows the selection of highly digestible plant tissues present in dicotyledoneous plants (Jarman 1974, Gordon and Illius 1988, Janis and Ehrhardt 1988). Thus, the feeding strategies of ungulates are thought to be the result of the interaction between food-quality and the constraints imposed by body size.

In this chapter I aim to characterise the feeding strategies of guanacos and sheep in the arid lands of Patagonia, by examining seasonal differences in their diets. In particular, I attempt to compare guanaco and sheep diets at three different levels of resolution: two levels of plant groups (first monocotyledoneous vs. dicotyledoneous plants, and second, plant functional types) as well as the level of individual plant species.

Like all camelid species, guanacos have adaptations to a "browser", selective feeding strategy, including a narrow incisor arcade (Janis and Ehrhardt 1988) and a high-motility digestive system (Hintz et al. 1973, Heller et al. 1984). However, guanacos have a body size (90 – 120 kg) within the range of intermediate feeders (feeding style 'c' proposed by Jarman, 1974, see section 1.2) and may be able to vary the proportion of dicotyledoneous plants and grasses (monocots) in their diet. Although sheep (50 - 80 kg, Merino breed) are smaller than guanacos, they have a relatively wide incisor arcade, typical of grazing ruminants (Gordon and Illius 1988), and a comparatively large digestive system adapted to delay the passage of food (Hofmann 1973, 1989). Consequently, sheep have been described as grazers (Hofmann 1989) but also as intermediate feeders (Janis and Ehrhardt 1988, Van Soest 1994).

The current theory for the diversity of feeding strategies in ungulates enables us to make firm predictions about the feeding ecology of guanacos and sheep under different hypotheses proposed by Hofmann and Jarman (see above). Firstly, if different feeding strategies are associated with different adaptations in the digestive system then according to Hofmann, guanacos will be predominantly browsers while sheep grazers. Thus, the proportion of dicotyledoneous plants in the diet of guanacos will be higher than in the diet of sheep. In contrast, if feeding strategies are primarily the result of body size, as proposed by Jarman (1974) and others, then both guanacos and sheep will be classified as intermediate feeders. In this case, both graminoids and dicotyledoneous plants will be important components of guanaco and sheep diets, and guanacos will be able to include a higher proportion of grass than sheep in their diet since guanacos are larger. Secondly, if guanacos are predominantly browsers and sheep predominantly grazers, I would not expect to find significant seasonal changes in their diets in terms of proportion of monocotyledoneous and dicotyledoneous plants. Whereas, if guanacos and sheep are both intermediate feeders then I expect them to increase the proportion of woody dicotyledoneous plants in their summer diet, when annual grasses and forbs are less available in the environment (see section 3.3). Thirdly, if guanacos are predominantly browsers and sheep grazers then they will include a relatively small proportion of the available plant species in their diet, and they will feed on different plant species. In contrast, if guanacos and sheep are both intermediate feeders they will be generalist herbivores including a high proportion of plant species in their diet. Finally, if guanacos are predominantly browsers and sheep grazers, then food niche overlap will be low in different seasons. Whereas, if guanacos and sheep are both intermediate feeders then food niche overlap will be high, particularly in summer when forage plants are scarcer than in spring.

4.2 MATERIALS AND METHODS

Faeces collection and treatment

Guanaco and sheep faeces were collected during spring and summer, in order that microhistological analysis (see below) might provide insights into the diet. Only fresh pellets were collected. Pellets were assumed to be fresh when they were wet, their colour was black and consistency soft. Pellets quickly desiccate in the heat and become brown and hard. Guanaco pellets were collected only from communal dung-piles in which the animals defecate and urinate. Because of their similarity, I did not assume all pellets found outside guanaco communal dung-piles were sheep pellets. Instead, sheep pellets were collected whenever sheep were observed to defecate or when fresh pellets were among sheep and no guanacos were present. Faeces were collected from up to three different pellet groups in the proximity (< 100 m) of the vegetation plots defined in Chapter 3 (immediately after surveying each plot). Sub-samples (different pellet groups) were pooled to give one sample per herbivore species per vegetation plot. As a result, the number of samples per herbivore species-site-season ranged from 3 to 12, totalling 110 samples for guanacos (49 in spring and 61 in summer) and 79 for sheep (39 in spring and 40 in summer) (Table 4.1). Faeces were air-drying in the field for up to one week and subsequently oven-dried for 48 hs at 60°C in the laboratory. Dried samples were ground to 1 mm in a Wiley mill.

Table 4.1: Number of faecal samples per herbivore species by site and season.

		Site								
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Spring	**Guanaco**	4	4	5	-	12	9	6	6	3
	Sheep	3	3	6	8	-	8	8	-	3
Summer	**Guanaco**	6	5	8	-	12	10	10	6	4
	Sheep	4	3	4	7	-	9	9	-	4

Microhistological analysis of faeces

Faeces were subjected to microhistological analysis by technicians at the National Institute of Agropecuarian Technology (INTA) in Bariloche, Argentina. Plant epidermal fragments in the faecal samples were identified at the level of genus or species when possible, and their frequency of occurrence recorded. Procedures for microhistological analysis followed the methodology proposed by Sparks and Malechek (1968). Five sub-samples were obtained from each sample, and 20 fields of each sub-sample were examined by microscope using 100 power-magnification. Overall, 100 fields for each sample and 189 samples resulted in 18,900 fields being examined.

The potential bias associated with the faecal microanalysis technique as an estimate of herbivore diet composition has been discussed extensively in the literature (Dearden et al. 1975, Vavra and Holechek 1980, Holechek et al. 1982). Differential digestibility may cause overestimation of shrubs and grasses in the diet and underestimation of the readily digested forbs (Kessler et al. 1981, Norbury 1988). However, when compared with other methods to study diet composition, including microanalysis of rumen samples, microhistological analysis of faeces provided similar results (Mohammad et al. 1995). In addition, faecal analysis detected more plant species than the rumen macroanalysis technique (Kessler et al. 1981). Although the most reliable technique to assess diet was reported to be the esophageal fistulation (McInnis 1976), faecal analysis is the most practical technique for evaluating dietary composition under field conditions. Furthermore, it also appears suitable for comparisons between species of herbivores. Although not "true ruminants", camelids, like ruminants, have a compartmentalised forestomach and regurgitate and remasticate their food. Moreover, there were no differences between guanacos and sheep in their efficiency in digesting perennial ryegrass (Fraser and Baker 1998). Therefore, in my study sites, I assumed that microhistological comparisons of faeces from the two species did not introduce systematic bias into the assessment of diet.

Diet composition and similarity

The diets of guanacos and sheep were analysed at three different levels of resolution: (a) monocotyledoneous, woody dicotyledoneous and herbaceous dicotyledoneous (forbs) plants; (b) plant functional types, comprising seven groups as defined in Chapter 3; and (c) key plant species. At the lowest level of resolution, the term "plant species" is used to refer to the maximum precision achieved in identifying plant fragments in the faeces (usually species but sometimes genera).

Differences in the proportion of individual plant categories between both herbivore species and seasons were analysed using t-tests (paired samples, with level of significance set to $p < 0.05$). Data is presented as percentage of each plant functional type (or species) in the faeces and assumed to represent the diet. Guanaco and sheep diets were compared by site and by season, using Kulcyznski's similarity index (Oosting 1956) to estimate the overlap in terms of percentage of different plant functional types and also plant species.

$$\mathbf{K = \sum^{n} [2\,(W.100) / (a_i + b_i)]} \qquad (1)$$

where

K: Kulcyznski's Similarity Index (%)

W: represents a_i if $a_i < b_i$, and b_i if $b_i < a_i$

a ; b: percent of functional type *i* or species *i* in the diet or in the environment *a* or *b*

Also, Kulcyznski's index was used to estimate within-species similarities between spring and summer diets and finally to estimate similarity between the percentage of functional types in the diets and their availability in the environment (see Chapter 3) as a general estimate of selectivity.

Diet selection

In addition to the Kulcynzski's similarity index to estimate general selectivity, specific dietary preferences of guanacos and sheep for plant functional types and species were estimated using Ivlev's electivity index (Ivlev 1961). The index compares the proportion of a particular plant species or group in the diet with the proportion available in the environment.

$$\mathbf{I_v = [(r_p - r_a) / (r_p + r_a)]} \qquad (2)$$

where

I_V: Ivlev's Electivity Index ($-1 < Iv < 1$)

r_P: proportion of plant category in the diet

r_a: proportion of plant category in the environment

Positive values indicate that the animals ate the plant type or species considered in a higher proportion than available in the environment (selection), while negative values indicate that the plant is underrepresented in the diet (avoidance). Zero values indicate that the animals ate a given species in proportion to its availability in the environment. In order to obtain clearer patterns of selection or avoidance, I defined an arbitrary "indifference" interval ranging from *–0.3* to *0.3* in the index value.

Statistical analysis

Statistical significance of dietary overlap, diet similarity between seasons and diet selection in relation to environmental availability were analysed by randomisation tests (Manly 1997). For every case, a matrix containing all possible similarity combinations was calculated (see Figure 4.1 as an example of interspecific dietary overlap).

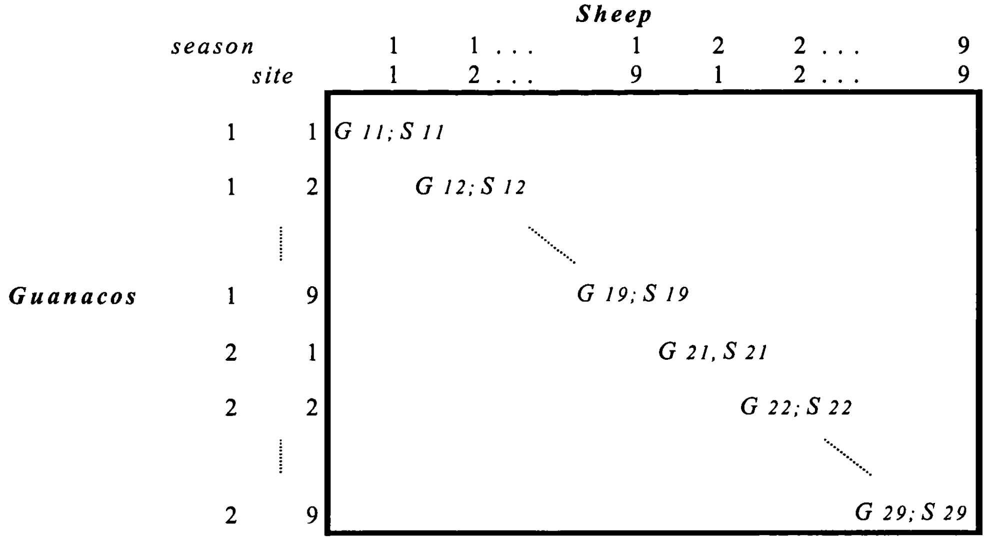


Figure 4.1. Schematic representation of the matrix used to study the significance of dietary overlap between guanacos and sheep. The diagonal represents overlap values between guanacos and sheep across sites and seasons (*Gij* = guanaco diet in season *i*, site *j*; *Sij* = sheep diet in season *i*, site *j*.) Mean overlap was compared against simulated means obtained through randomisation (see text below for details).

To test if the values of interest (see matrix diagonal) were significantly different from those expected at random, a programme in GENSTAT 5.3.2 was designed (see Appendix 3). After calculating the mean overlap or similarity across sites, the programme randomly altered the rows in the matrix and calculated the mean for every new diagonal. The simulation was run 500 times in each case. Mean overlap or similarity was accepted as significant if no more than 5 % of the means obtained through randomisation were higher than mean overlap or similarity ($s \leq 0.05$).

4.3 RESULTS

4.3.1 Seasonal variation in the diet of guanacos and sheep

Monocotyledoneous and dicotyledoneous plants

Guanacos: Mean percentage of monocotyledoneous plants in the faeces of guanacos was higher in spring than in summer (Table 4.2) and conversely the percentage of dicotyledoneous plants (woody and herbaceous combined) was significantly higher in summer than in spring ($t = -3.6$, d.f.=7; $p<0.001$). Considering dicotyledoneous plants alone, the percentage of woody plants in the diet of guanacos was higher in summer than in spring (Table 4.2) (range in summer: 21 to 56 %, range in spring: 8 to 39 %). Herbaceous dicotyledoneous (forbs) did not differ between spring and summer diets (Table 4.2).

Sheep: The percentage of monocotyledoneous plants in the faeces of sheep did not change significantly between spring and summer (Table 4.2). Likewise, the percentage of dicotyledoneous plants did not change between seasons ($t = 1.72$, d.f.=6; N.S.).

Table 4.2: Within species seasonal variation of monocotyledoneous and dicotyledoneous plants (bold) and functional types in the diet of guanacos and sheep. Values are percentage of plant groups in the diet (N.S.: non significant).

	Guanacos (d.f = 7)		**Sheep** (d.f. = 6)	
	Spring	Summer	Spring	Summer
% Monocotyledoneous plants	**64.9**	**45.3**	**40.6**	**44.0**
	t = 3.57, p < 0.01		t = -1.27, N.S.	
Perennial Grasses	47.7	40.0	29.1	40.2
	t = 1.14, N.S.		t = -3.7, p = 0.01	
Annual Grasses	17.3	4.4	11.6	3.7
	t = 7.36, p < 0.001		t = 2.81, p < 0.05	
% Woody dicotyledoneous plants	**17.4**	**36.6**	**27.8**	**33.9**
	t = -4.4, p < 0.01		t = -0.76, N.S.	
Evergreen Phanerophytes	11.4	20.9	12.0	19.5
	t = -3.32, p = 0.01		t = -1.35, N.S.	
Deciduous Phanerophytes	5.3	14.4	14.9	10.9
	t = -3.68, p < 0.01		t = 0.69, N.S.	
Chamaephytes	0.7	1.3	0.9	3.5
	t = -1.92, N.S.		t = -2.03, N.S.	
% Herbaceous dicotyledoneous plants	**16.6**	**17.2**	**30.9**	**19.5**
	t = -0.22, N.S.		t = 1.25, N.S.	
Perennial Forbs	3.5	12.7	4.2	13.3
	t = -5.59, p < 0.001		t = -1.92, N.S.	
Annual Forbs	13.1	4.6	26.7	6.3
	t = 3.79, p < 0.01		t = 2.7, p < 0.05	

Within the dicotyledoneous plants selected by sheep there were no significant differences in the proportions of neither woody plants nor forbs between seasons (Table 4.2).

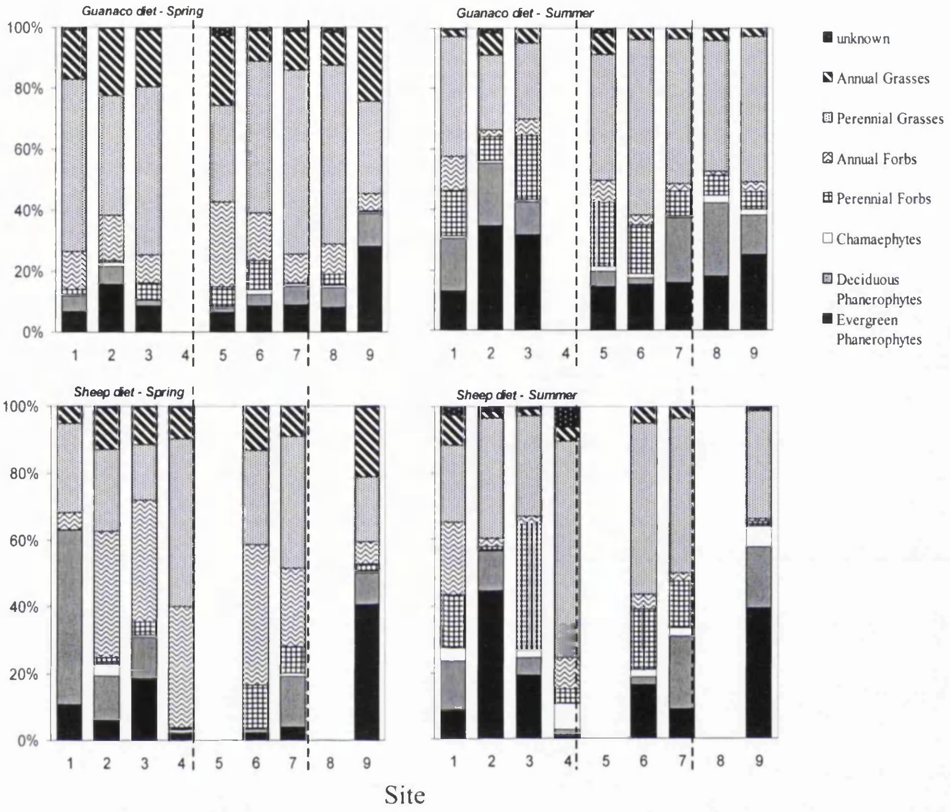
Plant functional types within monocotyledoneous and dicotyledoneous plants

Guanacos: The reduction in monocots in summer, described above, was largely due to a decrease in presence of annual grasses (Table 4.2). The increase in woody dicots in summer was general with the percentage of both evergreen and deciduous panerophytes doubling (Table 4.2). Although herbaceous dicots seem to be equally present in both seasons this concealed opposite trends in perennial forbs which increased significantly in summer, while annual forbs decreased significantly (Table 4.2).

Sheep: Although monocots made up a similar proportion of the diet in both seasons, this concealed an increase in perennial grasses in summer while annual grasses declined (Table 4.2). Like guanacos, sheep decreased the percentage of annual forbs in their diet in summer but this was not balanced by a significant increase in perennial forbs. The presence of each of the three woody dicots groups in the diet did not differ between seasons (Table 4.2).

Percentages of the seven plant functional types in the diets of guanacos and sheep across all sites in spring and summer are shown in Figure 4.2

Figure 4.2: Percentage of each plant functional type in the diet of guanacos and sheep across all sites in spring and summer (sites 1 to 4 are in the NE region, 5 to 7 in the SE and sites 8 and 9 in the Central region. Guanacos were allopatric in sites 5 and 8 while sheep were allopatric in site 4).



Key plant species

A total of 102 different vegetation species making up 79 genera and 38 families were identified across all regions. Both guanacos and sheep ate 73 species (71.6 %) grouped in 60 different genera (see Appendix 4). I found only three plant species eaten just by guanacos and six eaten just by sheep. Although most of the identified plant species in the environment were found in guanaco and sheep diet, only 17 plant species (genera or species level) represented at least 10 % of the diet of guanacos or sheep in any site-season combination and were considered key plant species (Table 4.3). In total, these 17 species accounted for 80 % of the plant fragments found in the faeces of guanacos and sheep.

Table 4.3: Mean (± S.E.) seasonal percentage of key plant species in the diet of guanacos and sheep, and seasonal differences within herbivore species (guanacos: d.f. = 7; sheep: d.f. = 6).

	Guanacos			***Sheep***		
	Spring	Summer		Spring	Summer	
Perennial Grasses						
Distichlis spp.	0.30	2.36	$t = -1.89$	0.67	3.67	$t = -1.75$
	(0.20)	(1.23)	*N.S.*	(0.40)	(2.01)	*N.S.*
Sporobolum rigens	0.31	1.22	$t = -1.47$	0.39	2.88	$t = -1.34$
	(0.22)	(0.72)	*N.S.*	(0.34)	(1.79)	*N.S.*
Stipa spp.	26.93	29.55	$t = -0.56$	18.72	26.71	$t = -3.15$
	(3.29)	(2.20)	*N.S.*	(3.48)	(3.93)	$p < 0.05$
Poa spp.	16.09	9.10	$t = 2.46$	6.93	6.86	$t = 0.05$
	(3.13)	(2.56)	$p < 0.05$	(1.82)	(2.08)	*N.S.*
Annual Grasses						
Schismus barbatus	12.63	2.58	$t = 5.10$	9.11	2.74	$t = 2.38$
	(2.33)	(0.66)	$p < 0.01$	(1.94)	(1.14)	*N.S.*
Evergreen Phanerophytes						
Atriplex spp.	0.53	0.56	$t = -0.08$	1.42	1.80	$t = -1.84$
	(0.38)	(0.23)	*N.S.*	(1.32)	(1.39)	*N.S.*
Condalia microphylla	0.00	1.45	$t = -1.51$	0.02	0.86	$t = -1.00$
		(1.27)	*N.S.*	(0.02)	(0.86)	*N.S.*
Junellia spp.	1.84	0.57	$t = 0.96$	1.46	1.83	$t = -0.64$
	(1.26)	(0.26)	*N.S.*	(1.34)	(1.23)	*N.S.*
Chuquiraga avellanedae	5.46	9.07	$t = -2.95$	5.06	8.48	$t = -0.85$
	(1.16)	(1.36)	$p < 0.05$	(2.14)	(3.97)	*N.S.*
Schinus spp.	2.46	9.20	$t = -3.90$	2.77	6.14	$t = -2.10$
	(0.67)	(2.20)	$p < 0.01$	(2.51)	(2.07)	*N.S.*
Deciduous Phanerophytes						
Ciclolepys genistoides	0.47	1.38	$t = -0.68$	12.16	0.06	$t = -3.51$
	(0.20)	(1.27)	*N.S.*	(6.99)	(0.05)	$p < 0.05$
Prosopidastrum globosum	0.30	5.66	$t = -2.87$	0.38	4.37	$t = -1.74$
	(0.18)	(2.04)	$p < 0.05$	(0.27)	(2.24)	*N.S.*
Prosopis spp.	0.03	3.22	$t = -1.75$	0.48	2.21	$t = -2.27$
	(0.03)	(1.79)	*N.S.*	(0.43)	(1.17)	*N.S.*
Perennial Forbs						
Perennial Chariophyllaceae	1.99	8.09	$t = -2.54$	1.16	11.61	$t = -2.52$
	(0.91)	(2.35)	$p < 0.05$	(0.58)	(4.32)	$p < 0.05$
Annual Forbs						
Duseniella patagonica	0.28	0.00	$t = 1.40$	2.98	0.83	$t = 1.08$
	(0.20)		*N.S.*	(1.67)	(0.75)	*N.S.*
Erodium cicutarium	9.97	2.14	$t = 3.88$	17.92	3.80	$t = 2.63$
	(1.74)	(1.04)	$p < 0.01$	(4.00)	(2.40)	$P < 0.05$
Plantago patagonica	1.06	0.58	$t = 0.75$	2.40	0.42	$t = 1.04$
	(0.64)	(0.22)	*N.S.*	(2.10)	(0.22)	*N.S.*

Guanacos: From spring to summer, guanacos significantly decreased the percentage of the perennial grass Poa spp., the annual grass Schismus barbatus and the annual forb Erodium cicutarium in their diet. In contrast, guanacos increased the presence of perennial dicots in their diet in summer as percentages of evergreen shrubs Chuquiraga avellanedae and Schinus johnstonii, the deciduous shrub Prosopidastrum globosum and the perennial Chariophyllaceae forbs were significantly higher than in spring (Table 4.3).

Sheep: There was an increase in the percentage of the perennial grass Stipa spp. and the perennial Chariophyllaceae forbs in the summer diet, and a decrease in the deciduous shrub Cyclolepis genistioides, the annual grass Schismus barbatus and the annual forb Erodium cicutarium (Table 4.3).

4.3.2 Within species – between season diet similarity

Plant Functional Types

Guanacos: As a result of the seasonal variation in diet composition, guanaco summer diet was different from the spring diet (not significantly similar in terms of the analysis, Table 4.4.b), either for sites with both guanacos and sheep living sympatrically or after adding sites 5 and 8 (no sheep).

Sheep: Although seasonal changes were not as pronounced as in guanacos, sheep diet was different between summer and spring in those sites shared with guanacos. However, mean similarity was significant after adding site 4 (no guanacos) to the analysis (Table 4.4.b). In site 4, between season similarity in sheep diet was 68 % (Table 4.4.a).

Key plant species

As for plant functional types, the diet of guanacos in terms of proportion of plant species was not significantly similar between spring and summer either for the six sites shared with sheep or for all sites with guanacos after including sites 5 and 8 (Table 4.4.b). In contrast, sheep consumed similar proportions of key plant species in spring and summer in sites shared with guanacos, and also after including site 4 (sheep only) in the analysis (Table 4.4.b).

Table 4.4: *a.* Similarity (Kulcyznski's index) between spring and summer diets of guanacos and sheep by site, for two different levels of resolution: plant functional types and plant species in the diet. *b.* Mean similarity between spring and summer diets of guanacos and sheep and significance (s) after randomisation tests. Sympatrically: results for six sites where both guanacos and sheep were present. All sites: results for all sites with guanacos (8 sites) or sheep (7 sites).

a

	Plant Functional Types		Plant Species	
Site	Guanacos	Sheep	Guanacos	Sheep
1	68	58	61	36.5
2	58	49	49.7	30
3	52	50	48.7	36
4	-	68	-	61
5	63	-	57	-
6	79	54	68.9	46.2
7	70	75	63.6	55.7
8	68	-	56	-
9	73	72	49	67.5

b

	Plant Functional Types				Plant Species			
	Sympatrically		All sites		Sympatrically		All sites	
Guanacos	66.7	N.S.	66.4	N.S.	56.85	N.S.	56.76	N.S.
Sheep	59.7	N.S.	60.9	s = 0.028	47.5	s = 0.002	45.3	s = 0.05

4.3.3. Herbivore differences in diet composition within season

Percentage of plant groups in guanaco and sheep diets are compared for sympatric sites (Table 4.5).

Spring: the percentage of monocotyledoneous plants was higher in the diet of guanacos than in sheep diet (Table 4.5). Within monocots, percentage of both perennial and annual grasses was higher in guanaco than in sheep diet (Table 4.5). Conversely, the overall proportion of dicotyledoneous plants was higher in sheep than in guanaco diet ($t = -5.42$, d.f. = 13, $p<0.01$). This was due to a higher percentage of annual forbs in sheep than in guanaco diet (Table 4.5). Whereas, mean proportions of woody dicots were not significantly different between guanaco and sheep, but herbaceous dicots (forbs) were more common in the diet of sheep than in guanaco diet (Table 4.5).

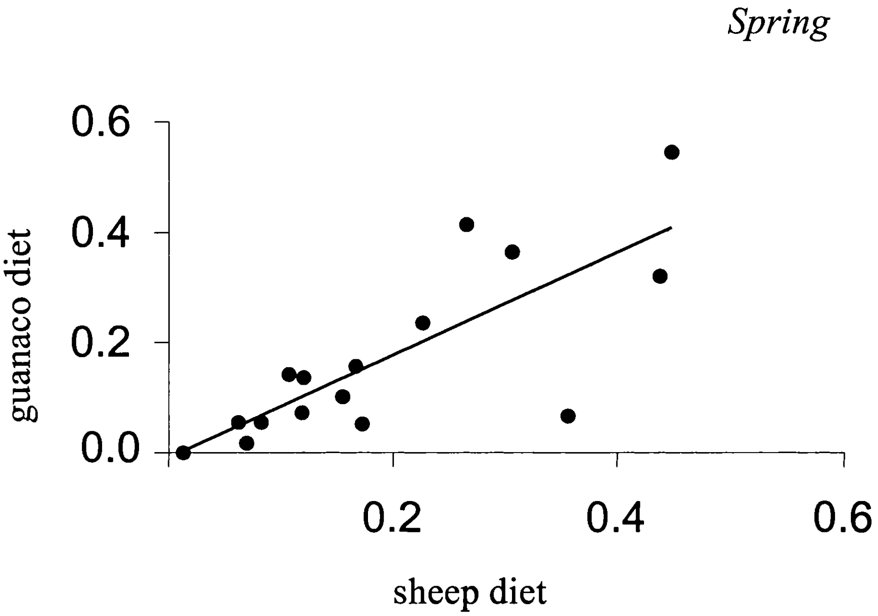
Summer: there were no significant differences in percentages of monocotyledoneous plants between guanaco and sheep diets in summer, as diets contained similar percentages of perennial and annual grasses (Table 4.5). Also, percentages of dicots were similar between guanaco and sheep diet ($t = -0.99$, d.f. = 13, N.S.) as percentages of woody dicots and forbs were not significantly different between guanaco and sheep diets (Table 4.5).

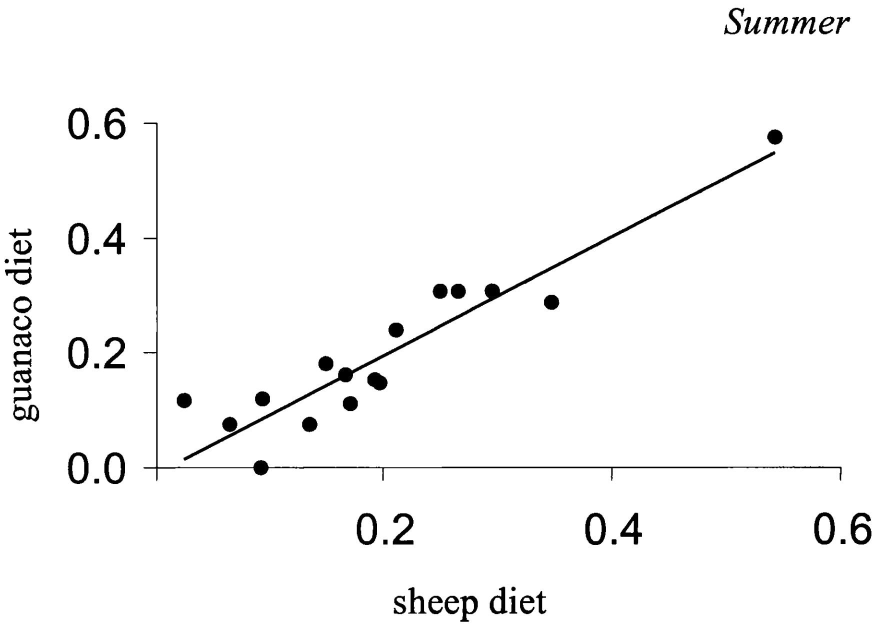
There was a strongly significant, positive correlation in the proportions of the 17 key plant species between guanaco and sheep diet, particularly in summer (correlation coefficients: spring = 0.80, summer = 0.92; Figure 4.3).

Table 4.5: Between species comparisons of proportions of plant groups in the diet in spring and summer. Values are mean percentage of plant groups in the diet for the six sites where guanacos and sheep were sympatric (t: t statistics for paired samples, d.f = 5 in all cases).

	Spring		Summer	
	Guanacos	Sheep	Guanaco	Sheep
% Monocotyledoneous plants	**65.9**	**37.5**	**44.6**	**39.6**
	t = 5.59, p < 0.01		t = 1.43, N.S.	
Perennial Grasses	48.5	25.6	40.5	36.0
	t = 5.60, p < 0.01		t = 0.99, N.S.	
Annual Grasses	17.4	11.9	4.1	3.6
	t = 2.66, p < 0.05		t = 0.00, N.S.	
% Woody dicotyledoneous plants	**19.2**	**31.9**	**37.8**	**37.8**
	t = -1.46, N.S.		t = 0.00, N.S.	
Evergreen Phanerophytes	12.8	13.7	22.5	22.7
	t = -0.24, N.S.		t = -0.05, N.S.	
Deciduous Phanerophytes	5.7	17.3	14.3	12.4
	t = -1.57, N.S.		t = 0.95, N.S.	
Chamaephytes	0.7	0.9	1.0	2.8
	t = -0.29, N.S.		t = -2.44, N.S.	
% Herbaceous dicotyledoneous plants	**14.2**	**29.9**	**16.9**	**20.5**
	t = -2.51, p = 0.05		t = -0.99, N.S.	
Perennial Forbs	3.0	4.8	12.3	14.7
	t = -0.02, N.S.		t = -0.73, N.S.	
Annual Forbs	11.2	25.1	4.6	5.8
	t = -2.38, p = 0.06		t = -0.54, N.S.	

Figure 4.3: Correlation between proportions of key plant species in guanaco and sheep diet by season (angular transformation of data values).





4.3.4 Dietary niche overlap between guanacos and sheep

Plant Functional Types

For the six sites where guanacos and sheep were sympatric, interspecific dietary overlap in terms of proportions of different plant functional types in the diet ranged from 49 to 84% in spring and from 76 to 93% in summer (Table 4.6.a). Although dietary overlap in spring tended to be high (s = 0.088, Table 4.6.b) it was not significant. However, there was very strong evidence of dietary overlap between guanaco and sheep diets in the summer (table 4.6.b).

Table 4.6: Dietary overlap between guanacos and sheep in terms of plant functional types and plant species found in the faeces during spring and summer for sites were both species were sympatric. Values are percentage overlap (Kulcyznski's index) in guanaco and sheep diet. *a.*Overlap by site by season. *b.* Mean overlap by season and statistical significance (s).

a

	Plant Functional Types		**Plant Species**	
Site	Spring	Summer	Spring	Summer
1	49.1	77.3	39.1	72.3
2	66	78.1	58.6	66.6
3	52.1	76.1	44.5	68.8
6	67.5	93.5	67.3	74.4
7	69	89.9	65.1	79
9	84.4	75.7	66.4	71.3

b

Plant Functional Types		**Plant Species**	
Spring	Summer	Spring	Summer
64.5	81.7	56.8	72.1
s = 0.088	s = 0.000	s = 0.018	s = 0.000

Key plant species

When percentages of the 17 key plant species were considered, mean overlap between guanacos and sheep was significantly high both in spring and in summer (Table 4.6.b). Furthermore, mean dietary overlap between guanacos and sheep was significantly higher in summer than in spring (t = -3.32, d.f. = 5, p = 0.02).

4.3.5 Feeding selectivity

General selectivity: Similarity diet composition - availability of plant functional types

Similarity indexes between proportions of plant functional types or species in the diet and the environment are shown in Table 4.7.a.

Spring: both guanaco and sheep diet composition was not similar to the availability of plant functional types in the environment in the six sites where guanacos and sheep were sympatric (Table 4.7.b). However, after sites 5 and 8 (no sheep) were added to the analysis then proportions of plant functional types found in guanaco diet during spring were significantly similar to the relative abundance of plant functional types in the environment (Table 4.7.b). Likewise, similarity between sheep diet and the environment was significantly high after site 4 (no guanacos) was added to the analysis (Table 4.7.b).

Summer: mean similarity between guanaco diet and availability of plant types in the environment was not significant either for 'guanacos & sheep' sites or 'all sites with guanacos' (Table 4.7.b). Similarity sheep diet-environment followed the same trend as in spring. Similarity was not significant in 'guanacos & sheep sites' but it was significant when site 4 was included (Table 4.7.b).

Table 4.7: *a*. Similarity between proportions of plant functional types in the diet and the proportion available in the environment (Kulcyznski's Index) by site by season. *b*. Mean similarity diet-environment and significance (s) for guanacos and sheep. *Sympatrically*: results for six sites where both guanacos and sheep were present. *All sites*: results for all sites with guanacos (8 sites) or sheep (7 sites).

a

Plant Functional Types

	Guanaco		Sheep	
Site	Spring	Summer	Spring	Summer
1	71	67	49	57
2	75	64	74	62
3	64	65	80	64
4	-	-	80	85
5	84	73	-	-
6	68	65	69	68
7	58	66	63	62
8	56	55	-	-
9	76	57	75	59

b.

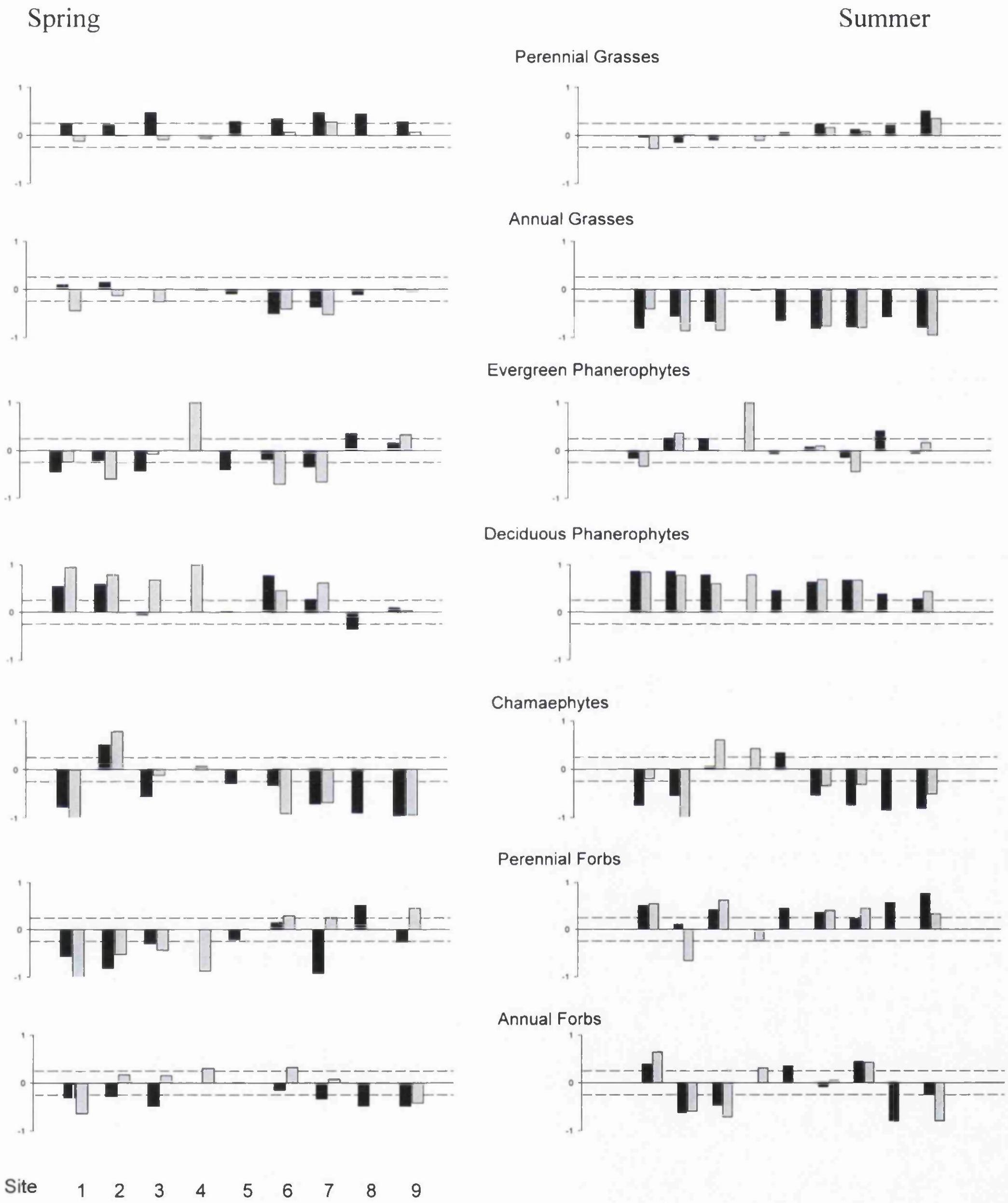
Sympatrically				***All sites with guanacos or sheep***			
Guanacos		Sheep		Guanacos		Sheep	
Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
68 N.S.	64 N.S.	68 N.S.	62 N.S.	69 s = 0.006	64 N.S.	70 s = 0.014	65.29 s = 0.018

Selection of individual plant functional types by guanacos and sheep

Guanacos: Considering the monocots, guanacos tended to select perennial grasses during spring but they were indifferent during the summer, and were generally indifferent to annual grasses in spring but strongly avoided them in summer (Figure 4.4). Evergreen phanerophytes tended to be avoided during spring but eaten in the same proportion they were available the summer. Guanacos showed no consistent patterns across sites for deciduous phanerophytes during spring, but consistently selected them during summer. Chamaephytes were generally avoided. There were no consistent patterns for perennial forbs during spring but they were selected in summer, while annual forbs tended to be avoided in most of the sites in both seasons (Figure 4.4).

Sheep: perennial grasses were eaten by sheep in the same proportion they were available in the environment, either in spring or in summer. Like guanacos, sheep were indifferent to annual grasses in spring and avoided them in the summer. Also sheep, like guanacos, tended to avoid evergreen shrubs during spring and were indifferent in summer, with the exception of site 4 where they strongly selected evergreen shrubs in both seasons. Sheep consistently selected deciduous phanerophytes, especially during the summer. Like guanacos, sheep generally avoided or ignored the dwarf-shrubs (chamaephytes) in both seasons. Also like guanacos, sheep showed no consistent trends towards perennial forbs in spring although they were generally selected in summer, and were indifferent to annual forbs in spring.

Figure 4.4: Selection for plant functional types across sites by season (Ivlev's Electivity Index, "indifference" interval was set from -0.3 to 0.3). guanacos ▬ sheep ▭



In general, for sites where guanacos and sheep were sympatric they showed similar selection patterns. There was no strongly opposed selection between guanacos and sheep either for or against a given plant functional type (Figure 4.4). In the reserve (site 5) where sheep were absent, guanacos were consistently non-selective during spring, consuming a diet in proportion to the availability of different vegetation functional types in the environment. Despite being also allopatric in site 8, guanacos were more selective than in site 5, clearly avoiding chamaephytic shrubs and annual forbs while preferring perennial forbs (Figure 4.4).

Selection of key plant species by guanacos and sheep

Given the earlier results, it was not surprising that guanacos and sheep showed similar patterns of selection for key plant species in their diet (Table 4.8). Although the perennial grass Stipa spp. was the most important in terms of percentage in guanaco and sheep diets, both herbivore species were indifferent in terms of selection patterns. The grass Poa spp. was slightly selected by guanacos, while sheep was indifferent. Guanacos and sheep were indifferent to the annual grass Schismus barbatus during spring and avoided it in summer. Both guanacos and sheep slightly avoided the evergreen shrub Chuquiraga avellanedae in spring, and both were indifferent during the summer. Other evergreen shrubs as Junellia spp. and Atriplex spp. were selected in spring and more strongly in summer by both herbivore species. Deciduous shrubs Prosopidastrum globosum and Prosopis spp. were avoided in spring by both guanacos and sheep and strongly selected in summer. Both guanacos and sheep were indifferent to the forbs Erodium cicutarium and perennial Chariophyllaceae in spring but strongly selective in summer, and both avoided the annual forb Plantago patagonica.

Table 4.8: Seasonal selectivity for key plant species by guanacos and sheep (Ivlev's Electivity Index, "indifference" interval was set from –0.3 to 0.3).

	Guanacos		***Sheep***	
	Spring	Summer	Spring	Summer
Perennial Grasses				
Sporobolum rigens	0.30	0.62	0.40	0.82
Stipa spp.	0.23	-0.02	0.05	-0.07
Poa spp.	0.47	0.41	0.09	0.29
Annual Grasses				
Schismus barbatus	0.20	-0.50	0.04	-0.48
Evergreen Phanerophytes				
Atriplex spp.	0.85	1.00	0.94	1.00
Condalia microphylla	-1	0.96	-0.30	0.94
Junellia spp.	0.57	0.72	0.49	0.90
Chuquiraga avellanedae	-0.32	-0.06	-0.36	-0.09
Schinus spp.	0.47	0.65	0.51	0.52
Deciduous Phanerophytes				
Ciclolepys genistoides	0.40	0.96	0.97	0.41
Prosopidastrum globosum	-0.36	0.78	-0.24	0.73
Prosopis spp.	-0.95	0.45	-0.43	0.29
Perennial Forbs				
Perennial Chariophyllaceae	0.08	0.76	-0.19	0.83
Annual Forbs				
Erodium cicutarium	0.04	0.88	0.32	0.93
Plantago patagonica	-0.68	-0.78	-0.40	-0.83

4.4 DISCUSSION

4.4.1 Feeding strategies

Diet composition and variation

My results suggest that both guanacos and sheep are intermediate feeders. As predicted from the Jarman hypothesis, both herbivore species included significant proportions of monocotyledoneous and dicotyledoneous plants in the diet. Contrary to the predictions derived from the Hofmann hypothesis about the role of anatomical differences in the digestive system on feeding strategies (Hofmann & Stewart 1972, Hofmann 1973, 1989; see description in *Chapter 1*), guanacos were not predominantly browsers nor sheep predominantly grazers. I found no evidence of sheep including less dicotyledoneous plants in their diet than guanacos. Instead, the percentage of dicotyledoneous plants in the diet of sheep tended to be higher than in the diet of guanacos during the spring season, when guanaco included more monocots than sheep in their diet. Therefore, sheep are not predominantly grazers in the arid lands of Patagonia but intermediate feeders including both monocotyledoneous and dicotyledoneous plants in their diet in similar proportions to those found in guanacos.

As predicted for an intermediate feeder, guanacos but not sheep increased the percentage of woody dicots in the summer diet. Guanacos seasonally changed the proportions of plant functional types and even the proportion of plant species within functional types. In contrast, sheep tended to eat the same proportions of monocots and dicots between seasons. Although sheep increased the percentage of perennial grasses and decreased the percentage of annual forbs and grasses in their diet from spring to summer, the diets were similar even in terms of plant species. As predicted for intermediate feeders, both guanacos and sheep were generalist herbivores including more than 75 % of available plants in the diet.

My results suggesting that both guanacos and sheep are intermediate feeders support the predictions of Jarman (1974) based on the relationship between body size and nutritional requirements in the guild of African antelope. Guanacos (90-120 kg) fall in the middle of Jarman's 50-200 kg category "c" of intermediate feeders in open habitats. Although smaller than guanacos, sheep also fall within the intermediate feeders category proposed by Jarman (1974).

The current work on guanaco feeding habits agrees with previous research in other parts of their range. For example, in La Payunia Reserve, a protected area in Mendoza, western Argentina, guanacos changed their diet from mainly grasses and forbs in summer to shrubs in winter, when the former decreased in quality and availability (Puig et al. 1996). Two studies in Tierra del Fuego described guanacos as generalist herbivores in a woodland-steppe ecotone. Guanacos included up to 61 % of grass and 30 % of forbs and shrubs plus epiphytes and lichens in their diet (Raedeke 1980). In a second study, guanacos varied the proportion of grasses in the diet from 38 to 90 % depending on the availability of dicotyledoneous plants (Bonino and Pelliza-Sbriller 1991).

Although sheep were classified by Hofmann (1989) as "bulk / roughage feeders" or grazers they are able to include more forbs and dwarf-shrubs in their diet compared to cattle (Grant et al. 1985, Hodgson et al. 1991). In an African nomadic pastoral ecosystem, sheep were clearly intermediate, generalist herbivores including up to 80 % of shrubs and forbs in the diet depending on the season (Coppock, Ellis and Swift 1986). Similarly, in the Australian dry rangelands sheep consumed less grasses and forbs and more shrubs during the dry season (Edwards et al. 1995). In the arid and semi-arid Patagonia, sheep diet composition included between 20 – 40 % of woody dicotyledoneous plants, especially during the dry summer (Pelliza-Sbriller et al. 1997).

In summary, my results agree with the prediction that both guanacos and sheep are intermediate feeders (in Jarman's 1974 classification) in the Patagonian steppe. Also, both species changed their diet seasonally although changes in the diet of guanacos were more pronounced than changes in sheep diet. The higher proportion of monocots in the diet of guanacos than in sheep diet during spring may be a consequence of guanaco larger body size, as larger animals are expected to tolerate lower-quality food in higher proportions than smaller animals (Demment and Van Soest 1985, Illius and Gordon 1991).

Comparative studies involving South American Camelids (SAC) are scarce, particularly for guanacos. In the pastoral system of the Altiplano region, San Martin (1987) found that sheep (40 kg body mass) had the highest dietary quality, in terms of *in vitro* dry matter digestibility, compared to alpacas (70 kg; intermediate dietary quality), while llamas (130 kg) had the lowest (see also San Martin and Bryant 1989 for a review). During foraging trials in the Scottish uplands, guanacos included less dicots and a higher proportion of dead material in their diet than did goats (Fraser and Gordon 1997a) and sheep (70 kg body weight, Welsh-Merino cross breed, Fraser and Baker 1998, Fraser 1998). Guanacos, as well as goats and sheep, maintained digestibility of organic matter in different seasons by changing diet composition and organic matter intake (Hodgson et al. 1991, Fraser and Gordon 1997b). Moreover, overall diet digestibility and voluntary intake were not significantly different between guanacos and sheep, contradicting the results of San Martin (1987) and San Martin and Bryant (1989) on llamas and sheep. Although it is difficult to extrapolate these results obtained on different SAC species, sheep breeds and different food qualities, they still suggest that the feeding strategies of guanacos and sheep are similar.

Diet selection

As predicted for intermediate feeders, guanacos and sheep are generalist herbivores capable of including in their diet a high proportion of the plant species available in the environment (see Appendix 3). However, both herbivore species have shown selectivity in terms of the plant functional types and species they ate (Figure 4.4, Tables 4.7 and 4.8). Just 17 out of 102 identified plant species represented up to 80 % of both species' diets. In sites where guanacos and sheep live sympatrically, guanacos were selective since their diet composition was not similar to the relative abundance of vegetation functional types in the environment, in neither spring nor in summer (Table 4.6.b). However, after the two sites where guanacos were allopatric were considered in the analysis, guanaco diet composition was similar to the availability of functional types during spring season. In fact, guanacos were particularly non-selective in terms of functional types in site 5, where there were no sheep (similarity diet-environment = 84 %, Table 4.7.a, Figure 4.2). A similar trend was found in sheep, since they showed a greater selectivity in sympatric sites but no selectivity when the allopatric site (site 4) was included in the analysis. Although similarity between sites 4 and 5 was relatively low (see Table 3.6 in *Chapter 3*), these results suggest an effect of sympatry on guanaco and sheep diet composition (in terms of plant functional types) that may lead to competition.

Selection patterns for particular plant functional types and plant species were generally similar for guanacos and sheep (Figure 4.4, Table 4.8). Furthermore, in a comparative study on diet selection of guanacos and sheep, conducted in the uplands of the United Kingdom, Fraser (1998) found that both species are selectively eat the green leaves of broad-leaved grasses. It has been argued that the morphology of the mouthparts impose constraints on selectivity, which are more severe in large animals, limiting the quality of the diet they can select (Illius 1997). Gordon and Illius (1988) found that grazers have a relatively wider incisor arcade than browsers but they increasingly diverge well above 100 kg in body weight. Mean incisor arcade breadth reported for sheep was 31.9 mm (Gordon and Illius 1988). Similarly, I estimated mean IAB = 31.4 mm (S.E. = 1.7, n = 8) for adult guanacos (Baldi, unpublished data). So it would seem that both guanacos and sheep are small enough to possess a relatively narrow incisor arcade which allow them to be selective. Moreover, intermediate feeders in open savanna and steppe habitats have the narrowest muzzles relative to body size (Janis and Ehrhardt 1988) although muzzle width itself does not allow one to distinguish intermediate feeders from grazers or browsers.

On the other hand, it is possible for different species with similar body weight and IAB to show niche separation. For example in the Serengeti, Murray and Brown (1993) suggested that growth stage of grass is primarily determining niche separation between three species. Topi (110 kg) and hartebeest (Alcelaphus bucelaphus, 125 kg) have an identical IAB of 50 mm, and together with wildebeest (160 kg, IAB = 70 mm) (Bell 1969) have all been classified as grazers feeding selectively on green leaves (Jarman 1974, see table 1.2 in *Chapter 1*). However, Murray and Brown (1993) found that each species in turn was more proficient in leaf selection and bite rate than the other two species, when grazing on a particular growth stage of grass. While wildebeest had a faster bite rate on early growth stages, topi were more selective for green leaf and had a faster bite rate at higher grass biomass, and hartebeest selected more green leaves on senescent swards.

The design of this study does not allow me to draw conclusions on diet selection beyond the plant species level. However, I suggest that the differences between guanacos and sheep in terms of body size are not large enough to result in differences in their incisor arcade breadth and hence in their ability to select plant functional types and species.

4.4.2 Variation in dietary overlap

As predicted for herbivores with similar feeding strategies, guanacos and sheep overlap in their diet, in terms of plant functional types and even in the plant species they select. Moreover, up to 80 % of the diets were made up by a few plant species present in similar proportions in guanaco and sheep diet. Diets were more similar in summer than in spring, due to changes in the diets of both herbivore species, especially in guanacos.

The changes leading to more similar diets in summer were largely due to an increase in the percentage of the grass Stipa spp in sheep diet, and an increase in the proportion of the deciduous shrubs Prosopidastrum globosum in guanaco diet. Also, there was a decline in the percentage of the deciduous shrub Cyclolepis genistoides in sheep diet from spring to summer.

Presumably the seasonal changes in the proportion of different plant species in the diet reflect changes in forage availability and quality (Owen-Smith 1992). It is well known that the nutrient content of grass declines as it matures while woody dicots continue to produce new leaves long after the rains ceased because they are deeper rooted (Noy-Meir 1973, Fischer and Turner 1978, Sala et al. 1989). In Patagonia, the percentage of crude protein in the grasses Stipa spp. and Poa spp. falls from 6-10 % in spring to 2-4 % in summer (Somlo et al. 1997). Some deciduous shrubs follow the same seasonal trend as grasses, showing pulses of assimilation closely related to short term rainfall (Bertiller et al. 1991). This is the case of Cyclolepis genistoides, important in the diet of sheep during spring and almost absent in the summer diet as its crude protein content falls from 5 to 1 %. Other deciduous shrubs like Prosopidastrum globosum, more important in guanaco summer diet than in spring, develop new leaves during the summer increasing its protein content from 5 to 9 % (Somlo et al. 1997). In addition, as was shown in Chapter 3, mean species richness was significantly lower in summer than in spring due mainly to the reduction in the number of annual forbs species together with a reduction in the relative availability of perennial forbs. Furthermore, from spring to summer there was a highly significant reduction in the percentage of green tissue in the herbaceous layer (perennial and annual grasses and forbs). Thus, changes in plant cover and availability of green tissue together with changes in food quality may be influencing seasonal diet composition and food niche overlap of guanacos and sheep.

My results on relative dietary overlap between guanacos and sheep changing with the seasons agree with studies on other mammalian herbivores. In the arid lands of Australia, dietary overlap between the bridled nailtail wallaby (Onychogalea fraenata), the black-striped wallaby (Macropus dorsalis) and domestic cattle was higher during the driest conditions, when all three species included more dicotyledoneous plants in their diet (Dawson et al. 1992, Ellis et al. 1992). In the same ecosystem, sheep and red kangaroos (Macropus rufus) increased their dietary overlap during dry periods (Dawson and Ellis 1994). While in North-America, dietary overlap between the pronghorn (Antilocapra americana) and domestic sheep was higher when both food abundance and quality decreased in winter (Schwartz and Ellis 1981).

This is the first study on diet composition and similarity of sympatric guanacos and sheep in the core of guanaco range. The only previous comparative study on guanaco and sheep diet was conducted in Tierra del Fuego where Raedeke (1979), analysing rumen samples, found that the overlap in terms of plant types increased from spring to summer (41 vs. 80 %). Also Raedeke (1979) reported that guanacos shifted their habitat preferences in the presence of sheep, although the evidence was circumstantial rather than the result of specifically designed studies. Nevertheless, Raedeke (1979) suggested that the introduction of domestic sheep in the guanaco range was the main cause in the drastic decline in guanaco numbers due to interspecific competition.

The abundance and distribution of ungulates are the result of interacting animal and environmental factors (Gordon 1989b, 1989c, Murray and Brown 1993). In the case of guanacos and sheep, both species are within the same feeding category and show similar dietary preferences in terms of the design of this study. These facts *per se* suggest a high potential for competition between guanacos and sheep for food resources (Belovsky 1986). In the following chapter I examine how sheep densities and vegetation composition affect the distribution of guanacos.

Chapter 5. SPATIAL AND TEMPORAL VARIATION IN THE DISTRIBUTION OF GUANACOS.

5.1 INTRODUCTION

The study of the distribution and resource use patterns among ungulate species has been a central issue in community ecology during the last 30 years (Schoener 1983, Tilman 1987, Hairston 1989, Putman 1996). Whether the guild of ungulate species within a given community is the result of interspecific competition, facilitation, predation or coexistence through resource partitioning has proved to be difficult to demonstrate since ideally it requires experimental manipulation (Schoener 1983, Wiens 1977, 1989, Hobbs et al. 1996, van der Wal et al. 1998). Instead, changes in the observed patterns of resource use have been frequently taken as an approach to the study of interspecific interactions (Sinclair 1979, Sinclair and Norton Griffiths 1982, Sinclair 1985, Gordon and Illius 1989, de Boer and Prins 1990, Putman 1996).

Competition is expected to result in the exclusion of a species or a change in the pattern of resources used in another species presence. In contrast, coexistence results from a fundamental difference in resources preferred, even in absence of interactions (Krebs 1994, Putman 1996), or when food is not limiting to herbivore populations (Belovsky 1986). It is difficult to know whether species coexistence is the evolutionary outcome of competition or coexisting species never competed because of their adaptations to use different resources (Begon et al. 1996). However, in my study system guanacos were the only large, native herbivore widely distributed across the Patagonian steppe until late in the 19th century when the domestic sheep were introduced.

Afterwards, guanaco populations declined precipitously, today occupying just 40 % of its aboriginal distribution range (Puig 1995). Competition for food between guanacos and sheep has been claimed to be a major cause of the demise of guanacos (Raedeke 1979), although legal hunting and poaching of guanacos has been considerable and also may have played a role (Franklin 1982, Cunazza et al. 1995). As I showed in the previous chapter, there were no substantial differences in feeding strategies or diet selection between guanacos and sheep. Furthermore, guanacos and sheep highly overlap in the proportions of plant species they select, particularly in the summer when food is comparatively scarce.

My aim in this chapter is to estimate and to account for the variation in guanaco densities across regions and sites, and between seasons and years. In particular, I will explore the relationships between guanaco and both sheep densities and the availability of the most important plant species in their diet (see *Chapter 4*).

I will use the term competition to refer to the occurrence of negative effects of one species on another, independently of the mechanisms (Law and Watkinson 1989, van der Wal et al. 1998). Although my approach to the study is largely comparative, several predictions can be made about the distribution of guanacos if competition with sheep exists (Belovsky 1984, de Boer and Prins 1990, van der Wal et al. 1998. First, if guanacos and sheep are competing then local densities of guanacos will be substantially higher in sites with no sheep compared to the density of guanacos in sympatric sites. Second, if competition occurs, guanaco densities will be inversely related to sheep densities. Third, changes in sheep densities due to management will result in changes in guanaco densities. Fourth, if guanacos and sheep compete then the density of guanacos in different populations will not necessarily depend on the environmental availability of the most important plant species in their diet in those environments.

5.2 MATERIALS AND METHODS

Animal surveys

Ground surveys of guanacos and sheep were conducted from an open pick-up vehicle with two observers standing in the back, following the line transect method (Burnham et al. 1980, Buckland et al. 1993). Observers within season were the same persons, and I participated in all the surveys. The first 15 surveys conducted in December 1996 were used as a pilot session and to define the survey design, therefore they were not included in the analysis. Replicated surveys were made travelling internal roads and tracks in every site during daylight hours (9:00-16:00hs). Between 2-6 surveys per site were conducted in three different sessions (total 120 surveys, 105 surveys considered for the analysis): one austral spring (1997) and two summers (1996-97 and 1997-98). Each region was visited twice per season in order to split the surveys in two sets to account for within-season variation (see table 5.1 for the distribution of surveys) although sometimes the timetable had to be altered due to bad weather conditions. Within visits to each site, surveys were repeated after two or three days (never on consecutive days) to minimise disturbance. Survey length ranged from 15 to 46 km depending on the site. Travelling speed varied between 10-30 km.h^{-1}. For every group of animals encountered the following data was recorded in pre-designed datasheets: (1) species, (2) number of animals, (3) distance from the vehicle and (4) angle from the observer. Distances from the vehicle were visually estimated at intervals of 0-50; 50-150; 150-300; 300-600; 600-1200 and more than 1200 m. Angle from the observer was estimated and assigned to one of 4 categories (0-20; 20-45; 45-75 and 75-90 degrees). Estimates of distances and angles were made always by myself to minimise variation due to the observer.

Table 5.1: Distribution of ground surveys for guanacos and sheep by region, site and season.

		Summer 1			Spring			Summer 2			
Region	Site	Dec '96	Jan '97	Feb '97	Sep '97	Oct '97	Nov '97	Dec '97	Jan '98	Feb '98	Mar '98
	1	2	3	1	2	3	-	3	-	2	
NE	2	2	3	1	3	3	-	3	-	2	
	3	-	1	1	3	3	-	3	-	2	
	4	-	1	1	3	1	-	3	-	2	
	5	-	2	-	-	3	3	-	3	-	2
SE	6	1	3	-	-	3	3	-	3	-	2
	7	-	1	-	-	3	2	-	3	-	1
	8	1	2	1	3	3	-	-	2	-	-
C	9	1	2	1	3	3	-	-	3	-	-

Manipulation of sheep numbers in the Central region

In March 1997, after the first summer season, all sheep in site 8 were removed by land-owners and taken to the adjacent site 9. Subsequently, there were no sheep in site 8 during the next spring (1997) and summer (1997-98) seasons.

Data analysis

Guanaco and sheep density estimates (animals.km^{-2}) were obtained using the DISTANCE software (Buckland et al. 1993, Laake et al. 1993). Each observation consisted of the number of individuals in a group and the perpendicular distance to the line of travel. Raw data was truncated to remove outlier distance values whenever the probability of detection was smaller than 0.15 (Buckland et al. 1993). One density estimate per census was obtained. Density estimates are obtained after fitting the data to a theoretical detection function. Selection of the detection function followed Akaike's Information Criterion (Akaike 1973), which uses likelihood ratio tests to identify the model that provides a good fit and minimises the number of parameters to estimate (Buckland et al. 1993). The uniform function was consistently the best fit for the NE and C region surveys data, while the half-normal detection function consistently provided the best fit for the surveys conducted in sites at the SE region. Density estimates for the SE region (Table 5.2) did not include site 5 (the reserve). As it was described in *Chapter 2*, its small area (12 km^2) and particular management conditions (no farming activities) are not representative of the regional conditions.

Variation in guanaco density was analysed using a generalised linear model (GLM). Guanaco density estimates followed a gamma distribution in accordance with Buckland et al. 1993. Estimates were weighted using the squared number of observations in each survey. Also, a log-link function was used in the GLM. The following is the maximal model designed to account for the spatial and temporal variation in guanaco densities:

Region*(SSp+SS)*Site + SiteDSh + SitePlants + SSDSh + SSSDSh

where:

Region: regions (NE, SE and C) as defined in *Chapter 2.*

Site: sites (1…9) as defined in *Chapter 2.*

Sum-Sp: contrast between the spring season and the two summers combined.

Sum1-Sum2: contrast between summer '96-97 and summer '97-98.

SiteDsh: Mean density of sheep per site (all seasons combined).

SitePlants: Mean ground cover of plant type or species per site (all seasons combined). Several functional types and plant species were separately fitted to account for the variation due to vegetation structure. The model shown in the *Results* section contains factors that significantly accounted for variation in guanaco densities: mean ground cover of the perennial grasses Stipa spp. and Poa spp. added together (Stipa+Poa), and mean total cover per site (SiteCover).

SSDSh: Mean density of sheep per Site by Season.

SSSDSh: Density of sheep per survey, within Site by Season.

+: Main effects.

*: Main effect plus interactions (i.e. A*B = A+B+A.B).

Significance of spatial variation due to sheep densities and plant cover was studied using Site as the error term, dividing the mean deviance of the factor by the mean deviance of Site (see Table 5.3). Also, factors accounting for temporal variation were tested dividing their mean deviances by the deviance of their interaction with sites (i.e. *Mean deviance Summer vs Spring / Mean deviance (Sumer vs. Spring) by Site*, see Table 5.3.f). Interaction effects *Region by Season* were tested against *Site by Season*.

5.3 RESULTS

5.3.1 Animal densities

Mean guanaco and sheep regional and local densities by season are shown in Table 5.2. At a regional scale, guanacos densities ranged from 2 to 9 animals.km^{-2} while sheep densities varied between 7 and 32 animals.km^{-2} depending on the season. At a local scale, guanaco densities were always lower than sheep densities in sympatric sites, varying between 1.3 and around 9 animals.km^{-2} depending on the season. In sites without sheep, guanaco densities were markedly higher than in the rest of the sites. In site 8, where sheep were removed after the first summer, I estimated a twofold increase to 17 guanacos.km^{-2} in the second summer. In site 5, the reserve without farming activities, the density of guanacos ranged from 34 to 44 animals.km^{-2} (an order of magnitude higher than in the rest of the sites). Sheep densities ranged from 4 to 80 animals.km^{-2}. The highest density of sheep was estimated for site 4, where no guanacos were seen in any survey.

Table 5.2: Regional and local densities of guanacos and sheep (per km^2 ± S.E.) by season.

Guanacos

	Site	Summer '96-97	Spring '97	Summer '97-98
NE		**1.98** (0.34)	**2.05** (0.41)	**1.75** (0.34)
	1	1.87 (0.35)	2.33 (0.20)	1.66 (0.57)
	2	2.83 (0.63)	3.87 (0.97)	3.35 (0.26)
	3	1.75 (0.10)	1.35 (0.17)	1.99 (0.56)
	4	0 (0)	0 (0)	0 (0)
SE[*]		**4.70** (1.35)	**3.51** (0.82)	**7.56** (2.04)
	5	37.82 (0.02)	33.64 (2.62)	43.86 (1.53)
	6	5.51 (1.39)	5.34 (0.98)	12.48 (1.13)
	7	1.44 (0.00)	1.31 (0.22)	1.40 (0.28)
C		**6.99** (1.36)	**6.21** (1.21)	**8.60** (3.51)
	8	8.48 (2.56)	8.98 (1.84)	17.04 (1.31)
	9	5.49 (0.81)	3.44 (0.21)	2.98 (1.03)

Sheep

	Site	Summer '96-97	Spring '97	Summer '97-98
NE		**25.57** (6.57)	**25.43** (6.20)	**27.07** (4.77)
	1	23.43 (9.74)	19.93 (4.73)	32.42 (4.53)
	2	11.07 (4.08)	10.39 (2.05)	26.22 (7.97)
	3	12.24 (2.03)	8.4 (2.03)	4.41 (1.41)
	4	49.97 (2.74)	80.43 (2.88)	45.24 (11.33)
SE[*]		**32.20** (6.17)	**26.47** (2.99)	**20.53** (2.71)
	5	0 (0)	0 (0)	0 (0)
	6	31.81 (10.66)	30.68 (4.25)	23.74 (2.05)
	7	32.99 (3.20)	21.43 (3.20)	17.32 (4.82)
C		**14.86** (2.46)	**6.51** (2.76)	**20.22** (8.53)
	8	17.76 (1.71)	0 (0)	0 (0)
	9	11.95 (4.08)	13.01 (4.07)	33.71 (3.88)

---

[*] *Mean density for the SE region do not include site 5 (see section 5.2)*

5.3.2 Variation in guanaco densities

Spatial variation

The density of guanacos varied significantly across regions and sites (Table 5.3.a). When mean density of sheep per site was added to the model, it accounted for 59 % of the spatial variation and it was negatively related to guanaco density (Table 5.3.b, Figure 5.1). After accounting for the variation due to sheep densities, regional effects were still significant (Table 5.3.b).

Table 5.3: Analysis of deviance of the GLM (see section 5.2) explaining the spatial variation in guanaco densities. (*d.f.* = degrees of freedom, *Deviance ratio (1)*: deviance ratios using Site as the error term for tests of significance, see section 5.2; *N.S.*: non significant). *a.* Spatial variation across regions and sites. *b.* Spatial variation after including mean sheep densities per site (SheepSite).

a.

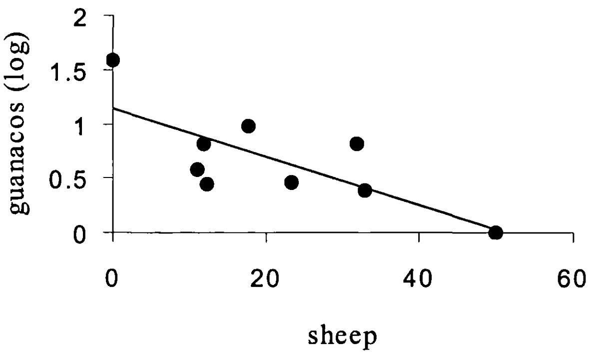
	d.f.	Deviance	Mean Deviance	Deviance ratio	
+ Region	2	27616.40	13808.20	178.64	$p<0.001$
+ Site	5	23508.29	4701.66	60.83	$p<0.001$
Residual	86	6647.60	77.30		
Total	93	57772.29	621.21		

b.

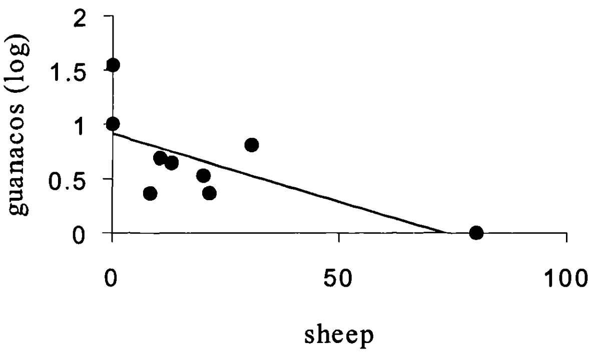
	d.f.	Deviance	Mean Deviance	Deviance ratio	Deviance ratio (1)	
+ SheepSite	1	30227.10	30227.10	391.05	30.62	$p<0.01$
+ Region	2	16948.80	8474.40	109.63	8.58	$p<0.05$
+ Site	4	3948.79	987.20	12.77		
Residual	86	6647.60	77.30			
Total	93	57772.29	621.21			

Figure 5.1: Spatial relationships between guanaco and sheep densities across sites by season (see Table 5.3b-d and text above).

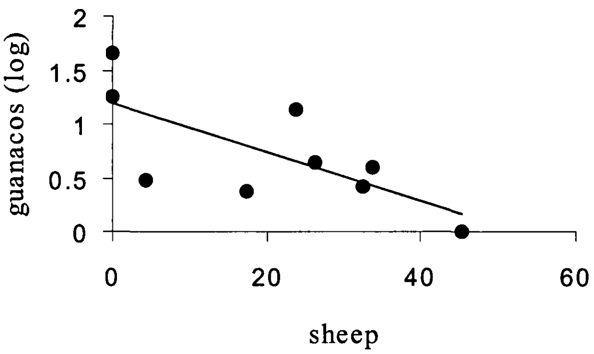
summer 96-97



spring 97



summer 97-98



Subsequently, mean availability per site of the two most important plant species in the diet of guanacos and sheep (see *Chapter 4* and section 5.2) were added to the model: the perennial grasses Stipa spp. and Poa spp. (Table 5.3.c). Mean availability of these plants by site explained 19.4 % of the spatial variation in the density of guanacos and together with sheep density they accounted for 78.5 % of the variation in density across regions and sites (Table 5.3.c). However, if Stipa spp. and Poa spp. are fitted before the density of sheep then the cover of perennial grasses accounted for most of the spatial variation in guanaco densities (Table 5.3.d). In both cases, the inclusion of the two variables (SheepSite and Stipa+Poa) resulted in regional effects becoming non significant (Table 5.3.c,d). When total vegetation cover per site was fitted instead of the grasses, it was also significant and together with the density of sheep per site explained 60.16 % of the spatial variation in guanaco density, although the remaining regional effects became significant again (Table 5.3.e). Spatial relationships between guanaco and sheep densities and plant cover of the dominant species in the diet are shown in Figure 5.2.

Figure 5.2: Mean density of guanacos and sheep (animals.km^{-2}, for all seasons combined) in relation to (*a*) availability of *Poa* and *Stipa* species across sites (expressed as the proportion of total vegetation cover), and (*b*) total vegetation ground cover (proportion).

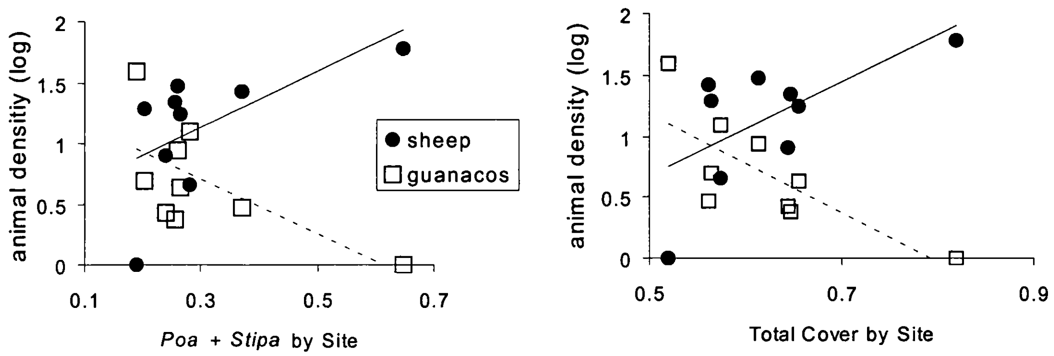


Table 5.3 (continuation): *c.* Spatial variation after including mean availability of grass species important in the diet (Stipa+Poa). *d.* Spatial variation after altering the order or explanatory factors. *e.* Spatial variation including total vegetation cover per site (Site Cover).

c.

	d.f.	Deviance	Mean Deviance	Deviance ratio	Deviance ratio (1)	
+ SheepSite	1	30227.10	30227.10	391.05	24.80	*$p<0.05$*
+ Stipa+Poa	1	6727.88	6727.88	87.04	5.52	*N.S.*
+ Region	2	10512.65	5256.33	68.00	4.31	*N.S.*
+ Site	3	3657.06	1219.02	15.77		
Residual	86	6647.60	77.30			
Total	93	57772.29	621.21			

d.

	d.f.	Deviance	Mean Deviance	Deviance ratio	Deviance ratio (1)	
+ Stipa+Poa	1	33655.62	33655.62	435.40	27.61	*$p<0.05$*
+ SheepSite	1	3299.36	3299.36	42.68	2.71	*N.S.*
+ Region	2	10512.65	5256.33	68.00	4.31	*N.S.*
+ Site	3	3657.06	1219.02	15.77		
Residual	86	6647.60	77.30			
Total	93	57772.29	621.21			

e.

	d.f.	Deviance	Mean deviance	Deviance ratio	Deviance ratio (1)	
+ SiteCover	1	29281.00	29281.00	378.81	25.79	*$p<0.05$*
+ SheepSite	1	1473.50	1473.50	19.06	1.30	*N.S.*
+ Region	2	16964.66	8482.33	109.74	62.75	*$p<0.01$*
+ Site	3	3405.53	135.18	14.69		
Residual	86	6647.60	77.30			
Total	93	57772.29	621.21			

Temporal variation and interaction effects

After accounting for spatial variation, the seasonal variation in sheep density by site accounted for 39 % of the temporal variation in guanaco density. Guanaco densities were negatively related to sheep densities within sites throughout time (Tables 5.3.f, Figure 5.3.). After accounting for the temporal variation due to sheep densities, guanaco densities varied significantly between spring and the two summers combined (overall density in spring = 7.16 guanacos per km^2, density in summer = 8.76 guanacos per km^2) but not between years (summer '96-97 vs. summer '97-98). However if *Summer 1 vs. Summer 2* is fitted before, this contrast becomes significant while *Summers vs. Spring* became non significant, suggesting that the overall density of guanacos significantly changes across the three seasons (Table 5.3.f). In fact, overall guanaco density (including site 5, the reserve) ranged from 6.02 guanacos.km^{-2} in summer '96-97 to 9.37 guanacos.km^{-2} in summer '97-98. Guanaco densities did not vary with sheep densities between surveys within site, within season. The only significant interaction was across regions between spring and summer (Table 5.3.f).

Total variation in guanacos densities

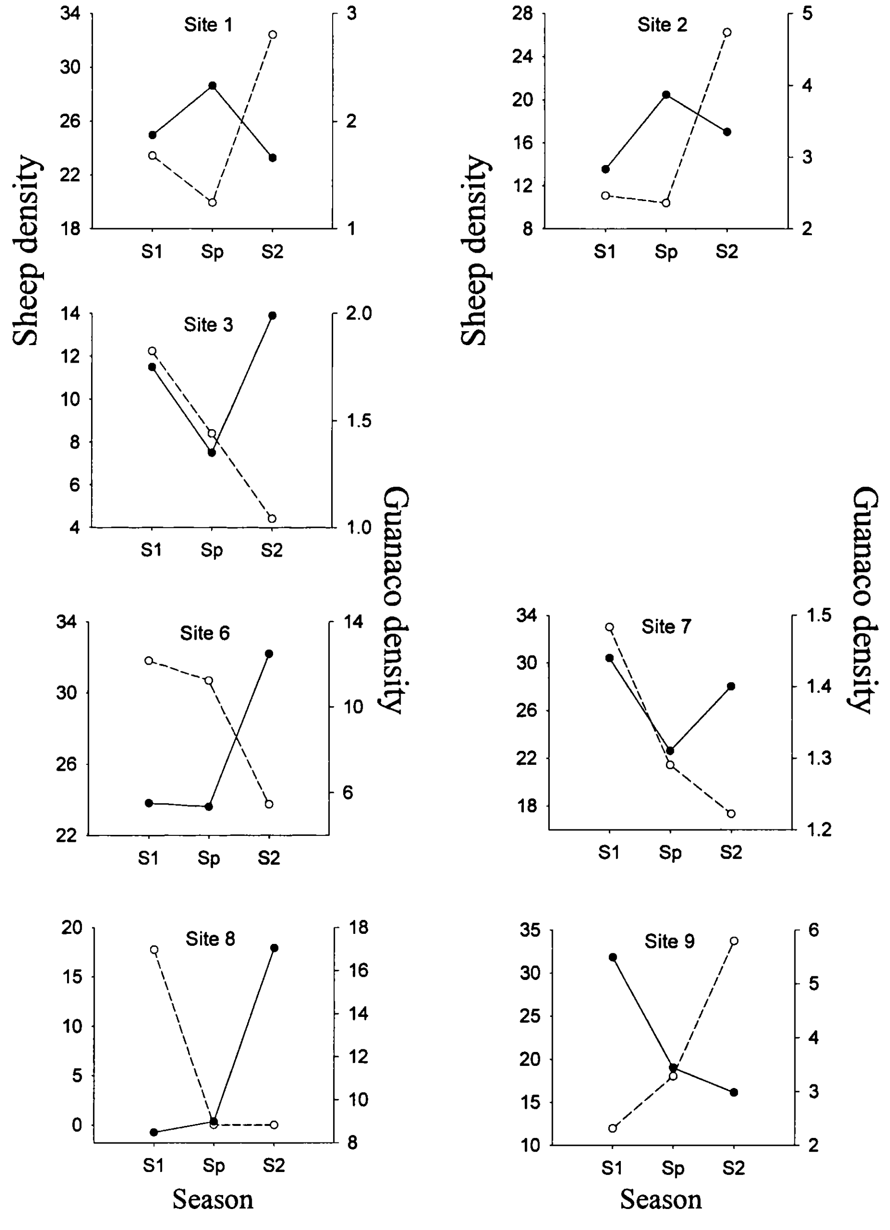
The general model explained 95 % of the variation in guanaco densities in space and time. Factors associated with spatial variation accounted for 93 % of the explained variation, while 5 % was explained by temporal associated factors and the remaining 2 % of the explained variation was due to interaction effects (Table 5.3.f).

Table 5.3 (continuation): *f.* Accumulated analysis of deviance including spatial and temporal variation and interactions.

	d.f.	Deviance	Mean Deviance	Deviance ratio	Deviance ratio (1)	
+ Sheep Site	1	30227.10	30227.10	727.81	24.80	*p<0.05*
+Stipa+Poa	1	6727.88	6727.88	161.99	5.52	*N.S.*
+Region	2	10512.65	5256.33	126.56	4.31	*N.S.*
+Site	3	3657.06	1219.02	29.35		
+SheepSS [(a)]	1	1114.41	1114.41	26.83	23.24	*p<0.01*
+Sum-Sp	1	1450.35	1450.35	34.92	177.52	*p<0.001*
+Sum1-Sum2	1	279.59	279.59	6.73	3.19	*N.S.*
+Sheep SSS	1	144.94	144.94	3.49		*N.S*
+Region by Sum-Sp	2	367.38	183.69	4.42	22.48	*p<0.01*
+Region by Sum1-Sum2	2	33.52	16.76	0.40	0.19	*N.S*
+Site by Sum-Sp [(b)]	5	40.86	8.17	0.20		*N.S*
+Site by Sum1-Sum2 [(c)]	4	350.87	87.72	2.11		*N.S*
Residual	69	2865.68	41.53			
Total	93	57772.29	621.21			

[(a)] Deviance ratio (1) for *SheepSS* significance test was obtained dividing its mean deviance by the average mean-deviance of (b) and (c). Then, Deviance ratio (1) = 1114.41 / (8.17+87.72)/2). Even if the highest, most conservative value is used as error term (87.72), the effect of *SheepSS* is still significant as Deviance ratio (1) = 12.7 > $F_{1,4}$; $p < 0.05$.

Figure 5.3: Within-site, seasonal variation in densities (animals.km^{-2}) of guanacos (solid lines) and sheep (dotted lines) in sympatric conditions, showing the strong negative associations between the two species. Sites 8 and 9 are contiguous paddocks in the same ranch where sheep were removed from site 8 and taken to site 9 (S1: summer '96-97, Sp: spring'97, S2: summer '97-98).



5.4 DISCUSSION

5.4.1 Animal densities and distribution

As predicted, guanaco densities were markedly lower than sheep densities in sympatric sites. Sheep were between 2 and 23 times more abundant than guanacos across the seven sites where both species lived sympatrically. In the reserve (site 5), where sheep was absent, the density of guanacos was an order of magnitude higher than in the rest of the sites. In sites 8 and 9 were sheep densities were "manipulated", the density of guanacos increased from 8.5 to 17 animals.km^{-2} in site 8 after sheep were removed and declined from 5.5 to 3 animals.km^{-2} in site 9 as sheep were added. These results agree with the prediction of differences in densities between sympatric versus allopatric sites under competitive interactions (Belovsky 1984, van der Wal et al. 1998). In Isle Royale National Park, Michigan, Belovsky (1984) estimated that densities of both moose (Alces alces) and snowshoe hare (Lepus americanus), were lower in sympatric than in allopatric conditions across islands. Belovsky (1984) suggested that resident hare populations limited moose colonisation rate through the use of shared food resources. In another study in New Zealand, Forsyth and Hickling (1998), interpreted that the lower densities of tahr (Hemitragus jemlahicus) and chamois (Rupicapra rupicapra) in sympatric compared to allopatric ranges as evidence of interspecific competition, even though no studies of habitat preferences were conducted. Although differences in densities may be due to differences in the resources preferred by guanacos and sheep, both species were broadly similar in terms of diet composition and food selection as I showed in *Chapter 4*.

Spatial variation

Across all nine sites, sheep densities alone accounted for almost 60 % of the spatial variation in guanaco densities. Also, guanaco densities were negatively related to the availability the most abundant plant species in their diet, the grasses Stipa spp. and Poa spp., and negatively related to total plant cover across sites (Figure 5.2). In contrast, sheep densities across sites were positively associated with *Stipa* and *Poa* combined, and with total plant cover (Figure 5.2). As shown in the previous chapter, *Stipa* and *Poa* combined represented between 39 and 43 % of the diet of guanacos and between 26 and 35 % of sheep diet. In addition, *Stipa* and *Poa* account for up to 98 % of the productivity of the herbaceous layer in arid and semi-arid Patagonia (Soriano et al. 1976). No guanacos were found in site 4 where sheep density, key plant species and total cover were all the highest. By far the highest density of guanacos was in site 5, the reserve, despite having the lowest total and key plant species cover. Although the general model may be strongly influenced by the extreme points in guanaco density at sites 4 (low) and 5 (high), the negative relationship between both species densities across sites is consistent with previous results obtained from aerial surveys of the NE region (Baldi et al. 1997), and agrees with other studies. For example, in the western highlands of Scotland, the presence of sheep apparently reduced the use of preferred swards by red deer hinds (Osborne 1984). Furthermore, across 48 parishes in the Scottish highlands, red deer densities were negatively related to sheep densities suggesting the possibility of competition for preferred vegetation communities (Clutton-Brock and Albon 1989).

Temporal variation

Seasonal variation in the density of sheep explained a large proportion of the variation in guanaco densities throughout time. Within sites, guanacos and sheep densities clearly followed opposed trends (Figure 5.3) particularly after one year (from summer '96-97 to summer '97-98). The trend was reinforced by the semi-experimental conditions in sites 8 and 9 in the Central region. As explained above (section 5.2), land-owners removed all sheep from site 8 after the end of the first season and released them in the neighbouring site 9. Although guanaco density did not increase immediately in site 8, there were twice as many guanacos a year later, during the summer '97-98. Likewise, the density of guanacos in site 9 was half of the density estimated during the previous summer. Therefore, my results suggest that guanacos are responding to changes in sheep numbers quite quickly.

Habitat shifts in ungulate species following changes in the density of domestic livestock have been reported for other communities. In an African savanna-woodland ecosystem, impala switched their habitat preferences avoiding paddocks with cattle during the dry, hot season and increased their foraging selectivity (Fritz et al. 1996). In Sierra Nevada, California, the presence of cattle induced female mule deer habitat shifts were observed (Loft et al. 1991). And, in Chilean Tierra del Fuego, direct observations have shown that guanacos shifted from using open grasslands in absence of sheep to greater use of forest patches when sheep were present in large numbers (Raedeke 1979).

The remaining temporal variation in guanaco densities may be the result of variation in the number of chulengos (calves). Densities were lower in spring than in summer during the breeding season. Also, the density of guanacos in the second summer (1997-98) was higher than the estimated one year before. By counting the number of new-borns, I estimated that only 4-6 % of the guanacos counted during the first summer were young of the year while the proportion increased to 15-20 % during the summer 1997-98. Although not shown in the results, proportions of different plant functional types and species by site by season were included in the model but none of them explained a significant proportion of temporal variation in the density of guanacos. It is likely that the spatial scale of this work was too large to detect changes in vegetation community use. Thus, seasonal changes in the density of guanacos were related to changes in sheep densities and possibly to differential guanaco breeding success.

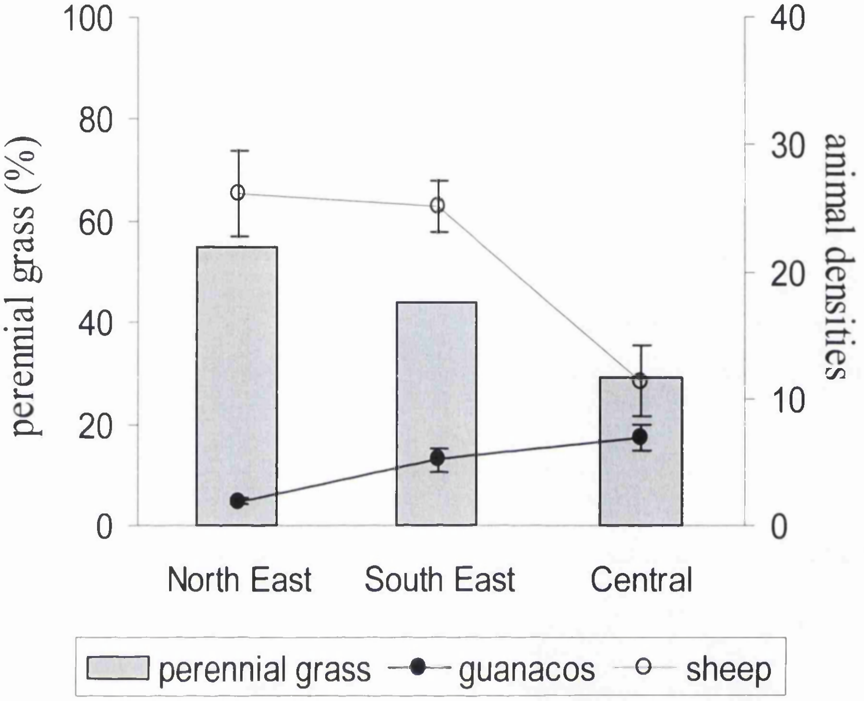
5.4.2 Are guanacos and sheep competing?

My results provide evidence to support several predictions on interspecific competition for food resources. First, the contrasting population densities of guanacos and sheep across sites together with the habitat shifts observed are all patterns consistent with predictions on interspecific competition processes (Belovsky 1984, de Boer and Prins 1990, Putman 1996, van der Wal et al. 1998). Second, both guanacos and sheep overlap in food resources (see *Chapter* 4) and possibly in habitat use, since soon after sheep were excluded from a site, this was occupied by guanacos. Overlap in habitat and food resources is a necessary requirement for interspecific competition to occur (Schoener 1974, Belovsky 1984, 1986, Wiens 1989, de Boer and Prins 1990). Third, my results suggest that sheep abundance is limiting the availability of food resources for guanacos, since sheep densities are positively related to the abundance of key forage plants, while guanaco densities are negatively related. Then, limitation by one species to the extent that food resources are used by another species is a negative effect expected under competitive interactions (Schoener 1974, Law and Watkinson 1989, Wiens 1989, de Boer and Prins 1990, van der Wal et al. 1998). Although this study was not designed to test for fitness effects on individuals (Hobbs et al. 1996a, 1996b) sheep densities appear to adversely affect affecting the densities of guanacos.

As described in the Introduction (*Chapter 1*), sheep were introduced in large numbers all over the Patagonian steppe where guanacos were the only large herbivores. Under food limiting conditions, it is expected that the introduction of another generalist herbivore of relatively similar body mass will result in interspecific competition for food (Belovsky 1986).

This is the first study on the factors affecting the distribution of guanacos occurring sympatrically with sheep. Previous studies were conducted in protected areas, where livestock were absent. For example, in Torres del Paine National Park, Southern Chile, guanacos spent more time in vegetation communities dominated by both grasses and forbs than in other communities where shrubs were the dominant vegetation type (Ortega and Franklin 1988). In La Payunia, a protected area in Mendoza, Argentina, guanaco abundance in different habitat types was positively correlated with the availability of preferred plant species, including grasses (Poa spp., Hordeum spp.), forbs (Erodium cicutarium, Quenopolum pappulosum) and shrubs (Hyalis argentea, Verbena spp.) (Puig et al. 1997). In contrast, my results suggest that the distribution of guanacos is primarily affected by sheep densities, resulting in a negative relationship between the density of guanacos and the availability of plant species important in their diet. Sheep farming seems to be primarily related to the most productive areas (Figure 5.4), since perennial grasses often dominate the steppe regions (Fischer and Turner 1978) accounting for up to two thirds of the primary productivity in arid lands (Fernandez et al. 1991).

Figure 5.4: Mean regional densities of guanacos and sheep (animals.km^{-2} ± S.E.) and percentage cover of perennial grasses.



Although this study was designed to explain the distribution of guanacos rather than of test interspecific competition, it provides strong evidence that guanacos are in conflict with sheep farming in the Patagonian steppe. Whether this conflict results from direct competition with sheep for forage resources, or indirect competition due to hunting and disturbance by humans is a matter requiring further investigation. It is likely that a combination of the above factors affected guanaco numbers and their distribution in Patagonia. Traditional European farming activities exported to Patagonia did not consider the use of native species as an alternative to domestic livestock production. Instead, guanacos were perceived as a problem for the development of sheep farming and therefore they were killed either by legal authorisation of provincial Governments or illegal hunting (Baldi et al. 1997).

In summary, sheep densities explain a significant proportion of variation in guanaco densities in space and time, suggesting the possibility of interspecific competition, either directly for food or indirectly due to human activities. Also, guanaco abundance was not positively related to the availability of key plant species in their diet. These results suggest that guanaco performance may be limited by sheep farming which has monopolised the most productive land.

Chapter 6. CONCLUDING DISCUSSION

6.1 THE DISTRIBUTION OF GUANACOS: A SHEEP-DEPENDENT SCENARIO

In this thesis, I have shown that guanacos and sheep feeding strategies are broadly similar, in terms of diet composition and selection. Yet surprisingly, guanaco densities were negatively related to the availability of the dominant plant species in their diet, the grasses *Stipa* and *Poa.* Sheep were between 2 and 23 times more abundant than guanacos across the sites where both species lived sympatrically. Across all nine sites, sheep densities alone accounted for almost 60 % of the spatial variation in guanaco densities. The highest guanaco density (34 - 44 animals.km^{-2}, an order of magnitude higher than in sympatric conditions) was estimated in site 5, the reserve, where sheep are absent. Conversely, the highest sheep density was found in site 4 (45 - 80 animals.km^{-2}), where guanacos were absent. Furthermore, within site variation in guanaco densities were negatively related to changes in sheep densities. This was particularly clear after removing all the sheep from site 8 and taking them to the neighbouring site 9. Guanaco density in site 8 quickly doubled, to become the highest outside the reserve where there were also no sheep, while numbers halved in site 9.

Thus, sheep densities rather than vegetation composition explained most of the variation in guanaco densities in space and time. Since both herbivores selected a similar diet, the negative correlation between guanacos and sheep densities cannot be the result of fundamental differences in the resources preferred by both herbivore species. Instead, interspecific competition with sheep is likely to play a role in the current distribution and abundance of guanacos.

6.2 THE POTENTIAL FOR COMPETITION

On the basis of nutritional requirements it has been argued that different species of relatively similar body mass and living in sympatry should be predisposed to interspecific competition for food (Schoener 1974, Belovsky 1986). The logic underlying this statement is that body mass has a major role in shaping foraging strategies (Bell 1970, Jarman 1974, but see *Chapter 1*). Therefore, similar sized herbivores should overlap in the use of food resources. In particular, under food limiting conditions, resource overlap is expected to result in interspecific competition (Wiens 1977, 1989, Belovsky 1984, de Boer and Prins 1990).

In this section, I will discuss the significance of the similarities in guanaco and sheep feeding strategies, presented in *Chapter 4*, stressing the importance of body size among the animal factors influencing ungulate foraging ecology. By doing this, I aim to show why guanacos and sheep are potentially competing species.

6.2.1 The underlying factors shaping guanaco and sheep feeding strategies

In my study area, neither of the herbivores are predominantly browsers nor grazers, but rather 'intermediate' feeders as predicted by Jarman (1974) on the basis of body size. Indeed, their diets were very similar in terms of plant functional types and in the proportions of the most important plant species eaten (see *Chapter 4*). These results do not agree with the predictions based on Hofmann's hypotheses that the feeding strategies of ungulates are primarily determined by anatomical adaptations in the digestive system (Hofmann and Stewart 1972, Hofmann 1973, 1989, see *Chapter 1*). Since Hofmann's description was based on species belonging to the order Ruminantia, it could be argued that the inclusion of guanacos (Tylopoda) is not valid to test Hofmann's hypotheses. However, guanacos are functional ruminants so they should not be an exception. Moreover, the main objective of my study on guanacos and sheep feeding strategies was not to test Hofmann's hypothesis *per se* but to set a comparative context to understand similarities and differences between both herbivore species. It is within this comparative context that guanacos and sheep feeding strategies do not match with the differences in their digestive system.

Although adult guanacos may be 30 – 50 kg heavier than sheep, both species are within the range of body size of intermediate selectivity (50 – 200 kg) proposed by Jarman (1974). Moreover, they have very similar incisor arcade breadth (IAB), which is consistent with their similar selective abilities. However, the larger body size of guanacos may enable them to tolerate a higher proportion of grass in their diet (Illius and Gordon 1991, Fraser and Gordon 1997a). In fact, I have shown that guanacos included a significantly higher proportion of perennial grass than sheep in their diet during spring (see *Chapter 4*). While guanacos might be selecting a slightly less digestible diet compared to sheep, the longer retention time in large animals should result in greater digestion and higher intake, allowing guanacos to obtain a higher proportion of their metabolic requirements from low quality food (Demment and Van Soest 1985, Illius and Gordon 1991, 1992).

Indeed, there seems to be no comparative evidence to support Hofmann's predictions about the extent to which differences in the digestive system should result in species differences in the feeding strategies. As it was described in *Chapter 1*, Gordon and Illius (1994) compared published data on the digestion kinetics in 21 species of African ruminants and found no differences in mean retention times in the gut between browsers, grazers and intermediate feeders after accounting for variation due to body mass and food type. Instead, the mass of digesta in the rumen scaled positively with body mass while the fermentation rate was negatively related to body mass, independently of the feeding habits proposed by Hofmann and Stewart (1972) (Gordon and Illius 1994). Also, by modelling published data on ruminants, Robbins et al. (1995) found that the ability to digest fibre was not associated with feeding style, as proposed by Hofmann (1973) but positively related to body size.

Although my study does not provide sufficient data to support unequivocally the hypothesis of Jarman (1974) and its implications, the results are much more consistent with it than with Hofmann's (1973, 1989) hypotheses about adaptations in the digestive system determining ruminant feeding strategies. Indeed, my results highly contradict the predictions of Hofmann's hypotheses.

6.2.2. The adaptive significance of body size

It has been argued that ungulate body size, influencing morphological and physiological attributes, is an adaptation to the constraints imposed by the variation in food availability (Illius 1997). As described in the previous section, larger animals can obtain a higher proportion of their nutritional requirements than small animals when feeding on abundant, poor quality food (Demment and Van Soest 1985, Illius and Gordon 1991, 1992). This logic can be extended within ungulate species. An example of the adaptive importance of body size in a changing environment was recently provided by Milner et al. (1999), working on Soay sheep in St Kilda, Scotland. In years with high over-winter mortality following severe food limitation, there was positive directional selection for females and lambs for large body size. Also, Milner et al.

(1999) found that positive selection for incisor arcade breadth was indirect, since it was positively correlated to body size.

If body size is the major animal factor affecting the nutritional ecology of ungulates, it is pertinent to ask what is the adaptive significance of the diversity in the ruminant digestive system described by Hofmann (1973). Although it still remains unclear, it is possible that adaptive changes in ungulate body size during their evolutionary history have overridden the importance of other morphological characteristics. Fossil evidence has shown that there was a trend towards increasing body size in ungulates from the late Eocene (35 – 40 million years ago) through the Oligocene and the Miocene (Janis 1997). This trend was related to the rapid spread of open grasslands in temperate regions, following the general decrease in temperature from the middle Eocene. Together with changes in body size, ungulate herbivores developed hypsodont (high-crowned) cheek teeth associated with the most fibrous diet of grasses (Janis 1995, MacFadden 1997). These trends are coincident with the evolutionary history of Camelids, which appeared in North America during the middle Eocene (40 – 45 million years ago). The earliest known Camelids, Protylopus petersoni (30 cm at the shoulder) and Poebrotherium wilsoni (60 cm) were both described as browsers since they had brachyodont (low-crowned) cheek teeth. Through the great diversification in the Miocene (15 – 20 million years ago) some forms reached 300 cm at the shoulder, and all developed hypsodont teeth (Gauthier-Pilthers and Dagg 1981, Franklin 1982). It was the llama-like *Hemiauchenia*, predominantly a grazer based on evidence from carbon isotopes in fossil teeth (MacFadden et al. 1996), who invaded South America by the beginning of the Pleistocene (2 million years ago) and diversified in today Camelid species. If changes in body size allowed Camelids to modify their feeding style and adapt to the changes in food availability, then the persistence of a digestive system apparently adapted to a "concentrate diet" might be due to a phylogenetic inertia, once selective pressures weakened after the marked increase in body size.

When guanacos spread across the South American arid lands, 10,000 years ago, they found no competitors, since most of the South American megafauna were already impoverished and became extinct at the end of the Pleistocene (Pascual 1996). Not until the last century, after the Europeans introduced the domestic sheep in Patagonia, was there a high potential for competitive interactions.

6.3 THE EVIDENCE FOR INTERSPECIFIC COMPETITION

6.3.1 Approaching the issue of competition

Under competitive interactions, individuals of one species might reduce the fitness of individuals of another species by limiting their access to a given resource, eventually leading to total habitat segregation (Schoener 1974, Pianka 1976, Schoener 1983, Law and Watkinson 1989, Wiens 1989, Hobbs et al. 1996a, 1996b). Unfortunately, interspecific competition is difficult to demonstrate with no designed experiments, but it is not usually feasible to conduct these on large animals. The only manipulative study designed to test interspecific competition in ungulates in the field is that by Hobbs et al. (1996a, 1996b), showing evidence of elk affecting cattle production (see *Chapter 1* and below).

More commonly, research on ungulates has approached the study of interspecific interactions by interpreting observed patterns of resource use (Sinclair 1979, Raedeke 1979, Belovsky 1984, Osborne 1984, Sinclair 1985, Belovsky 1986, Clutton-Brock and Albon 1989, Gordon and Illius 1989, de Boer and Prins 1990, Loft et al. 1991, Fritz et al. 1996, Forsyth and Hickling 1998). Also, this approach was frequently applied to the study of bird communities. For example, distribution patterns of different bird species in the New Guinean islands (Diamond 1975, 1978), and seasonal changes in diet and habitat use between species of Galápagos finches (Smith et al. 1978) were claimed to be the result of interspecific competition (see Schoener 1983 and Wiens 1989 for a review).

Investigating competitive interactions between African ungulates, de Boer and Prins (1990) argued that interspecific competition for food between two species is only possible where three conditions are met: (1) there must be habitat overlap, (2) species must share a common diet, and (3) food resources must be limited. As high habitat overlap in sympatric conditions might be possible in absence of competition (Vandermeer 1972, Strong 1983), it should occur when food availability is not limiting (Belovsky 1984). Accordingly, competing species must change their resource use patterns and distribution as a result of the interspecific interaction (Wiens 1989, de Boer and Prins 1990, Putman 1996). Therefore, it is expected that population densities of potentially competing species should be higher in habitats where species live allopatrically than in habitats where they live sympatrically (Belovsky 1984, 1986, van der Wal et al. 1998).

The logic proposed by de Boer and Prins (1990) allows *disproving* interspecific competition as a possible explanation of observed resource use patterns. Whereas, interspecific competition cannot be discounted *if* the above described conditions are met.

A different approach aimed to *demonstrate* interspecific competition was proposed by Wiens (1989). He developed a criteria consisting in a range of increasingly stronger types of evidence for interspecific competition (Table 6.1), including the elimination of alternative hypotheses. Although it may be difficult to fulfil, the criteria provided by Wiens (1989) are appropriate to examine the evidence resulting from studies on competitive interactions in a hierarchical fashion. In the following section, I will interpret my results within Wiens' (1989) context and provide further examples resulting from other studies involving ungulates. Where appropriate, I will refer to the conditions proposed by de Boer and Prins (1990).

Table 6.1: A scale of strength of evidence proposed by Wiens (1989) needed to demonstrate interspecific competition.

Strength of Evidence	*Type of Evidence*
Weak	**1. Observed patterns consistent with predictions** For example, contrasting population trends or shifts in resource use between sympatric and allopatric conditions.
↓	**2. Species overlap in resource use** If species do not overlap in resource use, competition in the past may have produced the divergence, but proximate competition is not likely.
↓	**3. Intraspecific competition occurs** Resource reduction should result in intraspecific competition first, since members of the same species are normally more similar to one another than they are to members of another species.
Suggestive	**4. Resource use by one species reduces the availability of resources for another species** If resource use by one species does not reduce the availability of that resource for another species, there will be no negative effects from the interaction.
↓	**5. One or more species is negatively affected** Negative effects on one or more species usually require manipulative experiments (i.e population densities) to assure that the effect on one species is related to the other.
Convincing	**6. Alternative process hypothesis should be ruled out** Alternative hypotheses must be tested, as any observed pattern is likely to be consistent with several possible processes of explanation.

6.3.2 The ghost of competition: following Wiens' criteria

Observed patterns consistent with predictions

The predictions for the distribution patterns of guanacos were that (1) local densities will be higher in sites with no sheep than in sympatric conditions, and (2) guanacos will respond to changes in sheep densities within sites (see section 5.1). My results showing a negative relationship between guanaco and sheep densities in space and time, resulting from contrasting densities in sympatric and allopatric conditions, agree with both predictions. Therefore, the evidence is consistent with the first condition proposed by Wiens (1989) about observed patterns (see Table 6.1).

Geographical separation and changes in habitat overlap as predicted from interspecific competition have been reported in many studies involving ungulates. In New Zealand, Forsyth and Hickling (1998) showed that densities of tahr were three times higher than chamois densities in 17 sympatric sites, while both species occurred at higher densities in allopatric sites. Sinclair (1979) found changes in habitat use and overlap in the Serengeti ungulate guild after the annual migration of wildebeest, consistent with interspecific competition. In the Lake Manyara reserve, northern Tanzania, de Boer and Prins (1990), reported that a high grazing pressure by elephants on a given vegetation patch takes place only in absence of high buffalo grazing pressure in preceding days. Habitat shifts were reported for impalas in the African savanna (Fritz et al. 1996), and female mule deer in California (Loft et al. 1991), both avoiding habitats with cattle during the hot, dry season. On the Isle of Rum, Scotland, red deer, cattle and ponies decreased habitat overlap in winter, after a decrease in food availability (Gordon and Illius 1989). Finally, in Tierra del Fuego, Raedeke (1979) observed habitat shifts in guanacos, from open grasslands to forest patches, after sheep increased in numbers. As discussed in the previous section, the observed distribution patterns of guanacos is consistent with the expected results from competitive interactions as proposed by Belovsky (1984, 1986), de Boer and Prins (1990) and Putman (1996).

Species overlap in resource use

Consistent with the second condition of Wiens (1989, see Table 6.1), guanacos and sheep overlap in resource use especially in summer. When food is scarce (*Chapter 3*) diet composition is more similar than in the spring season (*Chapter 4*). In Tierra del Fuego, Raedeke (1979) estimated a higher dietary overlap between guanacos and sheep in summer than in spring. Although I noticed that the occurrence of mixed guanaco and sheep groups was very rare at a small within-site scale (R. Baldi, pers. obs.), the spatial segregation in habitat might be temporary. It is likely that habitat overlap is potentially high, as my data showed guanacos occupying site 8 (with the highest density for the non-reserve sites) shortly after sheep were removed.

In the Serengeti, wildebeest, zebra, topi, buffalo and Thompson gazelles eat similar plant species within selected communities (Sinclair 1977) and showed high habitat overlap (Sinclair 1985). In Lake Manyara, de Boer and Prins (1990) did not estimate dietary overlap between buffalo and elephant, although they assumed overlap to be high based on previous work on buffalo diet (Prins and Beekman 1989) and elephant diet composition in other areas (Hofmann 1973, Jarman and Sinclair 1979). Although de Boer and Prins (1990) suggested that potentially competing species must overlap in habitat use, habitat overlap between elephants and buffalos was reported to be small both in the wet and dry seasons (de Boer and Prins 1990). On the Isle of Rum, Gordon and Illius (1989) estimated a high overlap between red deer, cattle and ponies using grass and forb communities with high live biomass during the summer, when forage resources are abundant (Gordon 1989b). Sheep and red deer hinds overlap in the use of short grass swards in the western Highlands of Scotland (Osborne 1984). In North America, the Rocky Mountain elk migrate during the winter from high altitudes to grassland communities in the lower valleys, overlapping with cattle in forage use (Hobbs et al. 1996a).

Intraspecific competition occurs

Although I do not have evidence of intraspecific competition, as proposed by Wiens (1989, see table 6.1), one would expect chulengo mortality to increase and female fecundity to decline in food limited conditions. In site 5 (the reserve without sheep), grass cover (perennial plus annual) increased from 9.8 % in summer 1996-97 to 59 % in the following summer. Over the same period, the percentage of chulengos at the end of the breeding season was only 3.5 % in the first summer (1996-1997)but increased to 22 % one year later. These annual differences were associated with a low total rainfall of 107 mm during 1996 (substantially lower than the mean of 250 mm), and 270 mm during 1997. Therefore, it is reasonable to suppose that the guanaco population in the reserve may face intraspecific competition for food resources.

In ungulates and other large animals, increased in calf mortality and reduced female fecundity, tends to be associated with density dependent intraspecific competition during periods of food shortage (Fowler 1987). However, studies testing both intraspecific and interspecific competition are very rare (Wiens 1989).

Resource use by one species reduces the availability of resources for another species.

The abundance of guanacos was negatively related to the abundance of *Stipa* and *Poa*, which make up 40 % of their diet. Sheep, often an order of magnitude more abundant than guanacos, were positively related to the abundance of *Stipa* and *Poa* across all sites. Furthermore, perennial grasses account for two thirds of the primary production in arid lands (Fernandez et al. 1991), with *Stipa* and *Poa* accounting for up to 98 % of the above ground biomass of grasses and forbs (Soriano et al. 1976). Guanacos might be excluded from the most productive habitats, which are monopolised for sheep farming. It is likely that farmers keep high sheep densities as long as the local productivity of forage species is sufficiently high. Overgrazing affects the structural patterns of vegetation reducing total plant cover and replacing highly palatable plant species by species of low palatability. Bisigato and Bertiller (1997) found that, at a high sheep grazing pressure, the reduction in perennial grass cover was mainly due to the decrease of Stipa tenuis, S. speciosa and Poa ligularis, all key plant species in the diet of guanacos and sheep. Also, large vegetation patches dominated by palatable shrubs and grasses were replaced by smaller patches with significantly lower species richness, dominated by the unpalatable shrubs Larrea spp. and dwarf shrubs (Bisigato and Bertiller 1997).

In Lake Manyara, Drent and Prins (1987) found a negative correlation in the proportion of grass consumed by buffalo and elephant populations through the year. Also, as the same trend was found in the short term (a scale of days), de Boer and Prins (1990) inferred that buffalos were reducing forage availability for elephants. In Scotland, Osborne (1984) suggested that high sheep densities may reduce the availability of some grass communities used by red deer hinds. Stronger evidence on resource limitation was obtained by Hobbs et al. (1996a) after manipulating elk densities in North America. At high elk densities in winter, standing crop of perennial grasses declined. Subsequently, daily forage intake by cattle (in terms of digestible energy and nitrogen) declined in direct relation to elk density.

One or more species is negatively affected

Although the abundance of guanacos is inversely related to sheep numbers, it is not clear whether guanacos are *directly* affected by sheep or *indirectly* by human activities associated with sheep farming. However, changes in sheep densities due to management can be taken as 'manipulative experiments' to some extent, particularly in the case of sheep moved from site 8 to 9, then the resulting negative response in the density of guanacos are in accordance with expected results under interspecific competition.

Most of the studies described in this section indicate the negative effects of interspecific competition based on observed patterns. In contrast, in the only controlled experiment on interspecific competition discussed here, Hobbs et al. (1996b) demonstrated a negative effect of high elk density on cattle production. Body mass of calves and cows declined significantly after forage availability was reduced, at high elk densities, below a minimum threshold value (Hobbs et al. 1996a, 1996b).

Are alternative processes ruled out?

Unfortunately, I cannot reject alternative hypotheses which may explain the distribution and abundance of guanacos. Predation and facilitation are alternative processes that have received special attention, and may potentially account for variation in the density of guanacos.

Predation: In my study area, the only natural predator, the puma (Felis concolor), has been virtually extirpated from the Patagonian steppe since the farming activities began one hundred years ago. However human activities, particularly legal culling and poaching of guanacos, have been considerable (Puig 1992). The lack of control even on legal culling (Baldi et al. 1997) makes it very difficult to obtain reliable data. In the meantime, culling has to be considered as a plausible explanation for the variation in guanaco population density.

In reality, other studies have similar difficulties. For example, Sinclair (1985) reviewed his former conclusion on competition (Sinclair 1979) considering that predation could be similarly important in structuring the Serengeti ungulate guild. Sinclair (1985) found that gazelles were spatially closer to wildebeest than expected by random, consistent with predictions from predation hypothesis. In addition, the marked decline of buffalo and elephant populations in areas close to human settlements, is associated with extensive poaching activities (Dublin et al. 1990). In Lake Manyara, de Boer and Prins (1990) interpreted that random visits by buffalo and elephant to preferred vegetation patches is not consistent with expected patterns of species association to dilute the risk of predation by lions (Panthera leo).

After accounting for culling rates, Clutton-Brock and Albon (1989) found that red deer densities across the Highlands were still negatively related to the density of sheep. Also, red deer densities significantly increased with altitude, as human activities decline (Clutton-Brock and Albon 1989). Therefore, although alternative processes like culling and human-associated activities are affecting the Highland populations, interspecific competition with sheep may play a fundamental role in red deer distribution.

Facilitation: Grazing facilitation has been claimed to be important in structuring herbivore guilds (Vesey-Fitzgerald 1960, Bell 1971), and occurs when grazing by one species improves the condition of the vegetation for subsequent grazing by a second species.

The most commonly cited example of facilitation occur in the Serengeti guild of ungulates. A grazing succession which would benefit zebra, wildebeest and Thomson's gazelle was described by Bell (1970), McNaughton (1976) and Maddock (1979), but data on population dynamics does not support this assumption (Sinclair and Norton-Griffiths 1982). In Lake Manyara, de Boers and Prins (1990) found a positive association in grazing pressure between wildebeest and zebra. However, this positive association consistent with facilitative processes may be also explained by the reduction of suitable habitat for both species (de Boer and Prins 1990). Stronger evidence on facilitation was obtained on the Isle of Rum, since cattle grazing in winter resulted in higher availability of green tissue for red deer during spring, and this was associated with an increase in the number of calves per hind in areas with cattle (Gordon 1988).

Facilitation is often linked to interspecific competition for food. For example, in a salt marsh in the island of Schiermonnikoog, The Netherlands, van der Wal et al. (1999) has demonstrated by manipulative experiments that Brent geese (Branta bernicla) benefited after winter grazing by brown hares (Lepus europaeus) retarded the vegetation succession. At the same time competition was induced, since after removing geese there was an increase in food availability enhancing the level of utilisation by hares (van der Wal 1998, van der Wal et al. 1999). Hobbs et al. (1996a, 1996b) found a facilitative effect since dead grass material removed by elk enhanced forage digestibility and nitrogen content. However, this effect was weak as high grazing pressures by elk reduced the daily intake of cattle. Therefore, Hobbs et al. (1996a, 1996b) found that positive effects were overridden by interspecific competition for food, especially when forage availability was low. Developing a mechanistic model, Illius and Gordon (1987) showed that larger animals can be excluded from swards where grazing pressure reduced sward height to a critical level, below which larger animals can not satisfy their nutritional requirements due to the limitation in food intake imposed by the incisor arcade breadth.

Is it possible that grazing facilitation occurs between guanacos and sheep? The only comparative, experimental studies involving guanacos were conducted in the United Kingdom. Bakker et al. (1998) found that bite depth of guanacos and sheep were similar across swards of three different heights. However, diet composition was different in guanacos and sheep because they selected different plant parts. Guanacos selected a higher proportion of dead leaf and stem than sheep (Bakker et al. 1998, Fraser 1998), and also than goats and red deer (Fraser and Gordon 1997a). Although the removal of dead material may increase the usage of green forage for sheep suggesting the possibility of grazing facilitation (Bakker et al. 1998), it is difficult to extrapolate these results. It is likely that the high grazing pressure by sheep in Patagonia reduced availability of green material for guanacos, particularly when food is limited.

In conclusion, I have shown evidence that guanaco distribution is negatively related to sheep density in relation to forage resources, consistent with criteria 1, 2, 4 and 5 in Wiens (1989) terms. Thus, I suggest that interspecific competition for food with the domestic sheep is influencing current guanaco distribution and population densities. While the evidence submitted here is suggestive, it is not conclusive since I cannot reject alternative explanations, criteria 6 in Wiens (1989) terms.

6.4 FUTURE RESEARCH AND IMPLICATIONS FOR CONSERVATION

6.4.1 Further research

The basic issues tackled in this study reflect the lack of information on guanaco population ecology in Patagonia. Further research is essential, both to increase the knowledge of guanaco populations and to underpin a management plan for a sustainable use of this species. Within-site work is needed to understand habitat selection patterns in relation to forage availability and between-species interactions at smaller scale. Research should include herbivore density-manipulation to assess the effects of grazing on food availability and herbivore productivity. Also, estimates of the nutritional properties of different forage types, diet digestibility and intake should provide a better understanding of the nutritional requirements of guanacos and sheep, needed to improve current management practices. In addition, it is essential to obtain demographic data in different guanaco populations. Natality and mortality rates, sex ratio and age structure are all poorly known, particularly in continental Patagonia under sheep farming conditions (Torres 1985, Puig 1992, Torres 1995).

6.4.2 Management recommendations

In the short term, it is recommended that (1) routine monitoring, as applied in this study, is continued and extended to more extensive surveys on guanaco subpopulations elsewhere; (2) issuing official permits for killing guanacos based on landowner's estimates should cease; (3) mechanisms controlling guanaco hunting should be implemented, and obtain reliable information on numbers, age category and sex of killed animals collected; (4) the main conclusions of this study and their implications should be discussed within Patagonian farming communities.

It is necessary to discuss alternatives to current farming activities, and to promote a change of attitude in the local communities in relation to indigenous wildlife in the longer term. Whilst marine mammals and birds are perceived as natural attractions and a benefit to the regional economy of Chubut, continental species like guanacos are seen as an obstacle to human development. Alternative strategies should be applied depending on local conditions, including controlled harvesting of guanacos, live shearing, tourist attractions on private ranches, and the creation of protected areas in the Patagonian steppe. All these issues have been very much neglected up to now and are worthy of further study.

Appendix 1: Analysis of variance for plant functional types cover across regions, contrasts between regions, sites, seasons (spring 1997, summer 1997-98) and interactions. See summary of results in section 3.3, tables 3.4 and 3.5. *Rest*: two regions combined contrasted against the third, *d.f.*: degrees of freedom, *s.s.*: sum of squares, *m.s.*: mean squares, *v.r.*: variance ratio, *F.pr.*: probability value.

Evergreen phanerophytes

```
Source of variation      d.f.       s.s.        m.s.     v.r.  F pr.
Region                      2    0.10172     0.05086     4.05  0.020
  C vs. Rest                1    0.05159     0.05159     4.11  0.045
  NE vs. SE                 1    0.05013     0.05013     3.99  0.048
Site                        6    3.48334     0.58056    46.25  <.001
Season                      1    0.00461     0.00461     0.37  0.546
Region.Season               2    0.01775     0.00888     0.71  0.495
(C vs. Rest).Season         1    0.00730     0.00730     0.58  0.447
(NE vs. SE).Season          1    0.01046     0.01046     0.83  0.363
Site.Season                 6    0.01702     0.00284     0.23  0.966
Residual                  138    1.73237     0.01255
Total                     159    5.35682
```

Deciduous phanerophytes

```
Source of variation      d.f.       s.s.        m.s.     v.r.  F pr.
Region                      2   0.710931    0.355465    50.26  <.001
  C vs. Rest                1   0.702184    0.702184    99.27  <.001
  NE vs. SE                 1   0.008747    0.008747     1.24  0.268
Site                        6   0.401868    0.066978     9.47  <.001
Season                      1   0.016267    0.016267     2.30  0.132
Region.Season               2   0.028140    0.014070     1.99  0.141
(C vs. Rest).Season         1   0.025585    0.025585     3.62  0.059
(NE vs. SE).Season          1   0.002555    0.002555     0.36  0.549
Site.Season                 6   0.012524    0.002087     0.30  0.936
Residual                  138   0.976094    0.007073
Total                     159   2.145825
```

Chamaephytes

```
Source of variation      d.f.       s.s.        m.s.     v.r.  F pr.
Region                      2    1.93445     0.96723    61.18  <.001
  C vs. Rest                1    1.93441     1.93441   122.35  <.001
  NE vs. SE                 1    0.00004     0.00004     0.00  0.961
Site                        6    0.30972     0.05162     3.27  0.005
Season                      1    0.00822     0.00822     0.52  0.472
Region.Season               2    0.02189     0.01094     0.69  0.502
(C vs. Rest).Season         1    0.00401     0.00401     0.25  0.615
(NE vs. SE).Season          1    0.01788     0.01788     1.13  0.289
Site.Season                 6    0.04153     0.00692     0.44  0.851
Residual                  138    2.18182     0.01581
Total                     159    4.49763
```

Perennial grasses

```
Source of variation      d.f.       s.s.        m.s.     v.r.  F pr.
Region                      2    2.25406     1.12703    50.40  <.001
  NE vs. rest               1    1.90073     1.90073    85.00  <.001
  C vs. SE                  1    0.35333     0.35333    15.80  <.001
Site                        6    4.27151     0.71192    31.84  <.001
Season                      1    0.43257     0.43257    19.34  <.001
Region.Season               2    0.18684     0.09342     4.18  0.017
(NE vs. rest).Season        1    0.08534     0.08534     3.82  0.053
(C vs. SE).Season           1    0.10150     0.10150     4.54  0.035
Site.Season                 6    0.05972     0.00995     0.45  0.844
Residual                  138    3.08589     0.02236
Total                     159   10.29060
```

Appendix 1: continuation

Perennial forbs

```
Source of variation    d.f.       s.s.       m.s.     v.r.  F pr.
Region                    2   0.857126   0.428563    61.69  <.001
  C vs. Rest              1   0.819669   0.819669   117.99  <.001
  NE vs. SE               1   0.037458   0.037458     5.39  0.022
Site                      6   0.246328   0.041055     5.91  <.001
Season                    1   0.039131   0.039131     5.63  0.019
Region.Season             2   0.007876   0.003938     0.57  0.569
(C vs. Rest).Season       1   0.006669   0.006669     0.96  0.329
(NE vs. SE).Season        1   0.001206   0.001206     0.17  0.678
Site.Season               6   0.108358   0.018060     2.60  0.020
Residual                138   0.958663   0.006947
Total                   159   2.217484
```

Annual grasses

```
Source of variation    d.f.       s.s.       m.s.     v.r.  F pr.
Region                    2    1.22379    0.61190    21.62  <.001
  SE vs. Rest             1    1.19307    1.19307    42.16  <.001
  NE vs. C                1    0.03073    0.03073     1.09  0.299
Site                      6    0.88471    0.14745     5.21  <.001
Season                    1    0.00100    0.00100     0.04  0.851
Region.Season             2    0.16789    0.08394     2.97  0.055
(SE vs. Rest).Season      1    0.07098    0.07098     2.51  0.116
(NE vs. C).Season         1    0.09691    0.09691     3.42  0.066
Site.Season               6    0.19645    0.03274     1.16  0.331
Residual                138    3.90523    0.02830
Total                   159    6.37908
```

Annual forbs

```
Source of variation    d.f.       s.s.       m.s.     v.r.  F pr.
Region                    2    0.31054    0.15527    10.03  <.001
  SE vs. Rest             1    0.21856    0.21856    14.11  <.001
  NE vs. C                1    0.09198    0.09198     5.94  0.016
Site                      6    0.43045    0.07174     4.63  0.001
Season                    1    3.70658    3.70658   239.37  <.001
Region.Season             2    0.28145    0.14072     9.09  <.001
  SE vs. Rest.Season      1    0.27999    0.27999    18.08  <.001
  NE vs. C.Season         1    0.00146    0.00146     0.09  0.759
Site.Season               6    0.12842    0.02140     1.38  0.227
Residual                138    2.13688    0.01548
Total                   159    6.99432
```

Total cover

```
Source of variation    d.f.       s.s.       m.s.     v.r.  F pr.
Region                    2    0.90365    0.45183    22.79  <.001
  C vs. Rest              1    0.55293    0.55293    27.88  <.001
  NE vs. SE               1    0.35072    0.35072    17.69  <.001
Site                      6    0.67499    0.11250     5.67  <.001
Season                    1    0.01604    0.01604     0.81  0.370
Region.Season             2    0.20039    0.10019     5.05  0.008
  C vs. Rest.Season       1    0.04668    0.04668     2.35  0.127
  NE vs. SE.Season        1    0.15370    0.15370     7.75  0.006
Site.Season               6    0.06910    0.01152     0.58  0.746
Residual                138    2.73649    0.01983
Total                   159    4.60066
```

Appendix 2: Identified plant species in the study area and their presence by region

		Presence in the Environment		
Evergreen Phanerophytes		NE	SE	C
ANACARDEACEAE	*Schinus johnstonii*	*	*	*
ASTERACEAE	*Brachyclados megalanthus*	*		*
	Chuquiraga avellanedae	*	*	*
	Chuquiraga hystrix	*		*
	Nardophyllum obtusifolium		*	*
CHENOPODIACEAE	*Atriplex lampa*	*		*
VERBENACEAE	*Junelia aff alatocarpa*	*	*	*
ZYGOPHYLLACEAE	*Larrea divaricata*			*
	Larrea nitida			*
	Berberis heterophyla		*	
	Colliguaya integerrima		*	
Deciduous Phanerophytes				
ASTERACEAE	*Brachyclados licioides*		*	
	Cyclolepis genistoides	*	*	*
	Psila spartioides		*	
EPHEDRACEAE	*Ephedra ochreata*	*	*	*
FABACEAE	*Prosopidastrum globosum*	*	*	*
	Prosopis alpataco	*	*	*
	Prosopis denudans	*	*	*
NICTAGINACEAE	*Bouganvillea spinosa*			*
OLEACEAE	*Menodora robusta*	*		*
RHAMNACEAE	*Colletia hystrix*		*	
	Condalia microphylla	*		*
SOLANACEAE	*Lycium spp.*	*	*	*
Chamaephytes				
ASTERACEAE	*Baccharis crispa*	*		
	Baccharis darwini	*	*	*
	Brachyclados caespitosus		*	
	Chuquiraga aurea	*	*	
	Chuquiraga erinacea	*	*	
	Nassauvia glomerulosa	*		
	Nassauvia ulicina	*	*	
	Senecio mustersii			*
FRANKENIACEAE	*Frankenia patagonica*	*	*	
ROSACEAE	*Acaena platyacantha*	*	*	
	Tetraglochin caespitosum	*		
UMBELLIFERAE	*Mulinum spinosum*	*	*	*
VERBENACEAE	*Acantholippia seriphioides*	*	*	*
	Junelia seriphioides			*

Appendix 2: continuation

		Presence in the Environment		
		NE	*SE*	*C*
Perennial Grasses and Graminoids				
CYPERACEAE	*Carex sp.*	*		*
	Eleocharis sp.	*		
POACEAE	*Distichlis spp.*	*	*	
	Festuca pallescens		*	
	Hordeum sp.	*	*	*
	Poa ligularis	*	*	*
	Sporobolus rigens	*	*	*
	Stipa chrisophylla		*	*
	Stipa longilumilis	*	*	*
	Stipa neaei	*	*	*
	Stipa pampeana	*	*	*
	Stipa speciosa	*	*	*
	Stipa tenuis	*	*	*
Perennial Forbs				
ASTERACEAE	*Baccharis melanopotamica*	*		
	Gamochaeta aff. stachidifolia	*	*	
	Grindelia chiloensis			*
	Perezia recurvata	*	*	*
	Psila tenela	*	*	
	Senecio gillesii	*	*	
	Taraxacum officinale	*		
CALYCERACEAE	*Boopis anthemoides*	*	*	*
CARIOPHYLLACEAE	*Cerastium arvense*		*	
	Herniaria cinerea	*	*	*
	Aff. Paronychia sp.	*		*
	Spergula ramosa	*	*	
	Spergularia sp.	*	*	
FABACEAE	*Adesmia villosae*			
	Astragalus moyanoii	*		*
	Hoffmansegia erecta			*
	Hoffmansegia trifoliata	*	*	*
IRIDACEAE	*Sisirinchium junceum*	*	*	*
POLEMONACEAE	*Gilia laciniata*	*	*	*
PORTULACACEAE	*Calandrina colchaguensis*	*		*
SANTALACEAE	*Arjona tuberosa*	*	*	*
SCHROPULARIACEAE	*Calceolaria sp.*	*		*
	Cardionema ramosissimmum	*	*	
Annual Grasses				
POACEAE	*Bromus brevis*	*	*	
	Bromus sp.		*	*
	Bromus trinii	*	*	*
	Schismus barbatus	*	*	*
	Vulpia spp.	*	*	*

Appendix 2: continuation

		Presence in the Environment		
Annual Forbs		*NE*	*SE*	*C*
ASTERACEAE	*Duseniella patagonica*	*		
	Facelis retusa	*	*	*
	Senecio chrysocomoides	*		
BRASSICACEAE	*Lepidium mirianthum*	*	*	
CARIOPHYLLACEAE	*Arenaria aff. Serpillifolia*		*	
	Cerastium junceum	*		*
	Spergula villosa		*	*
CONVOLVULACEAE	*Dichondra microcalyx*	*		
CRUCIFERAE	*Capsella bursapastoris*		*	
	Draba australis	*	*	*
FABACEAE	*Adesmia smithii*	*	*	
	Vicia pampicola	*	*	
GERANIACEAE	*Erodium cicutarium*	*	*	*
HYDROPHYLLACEAE	*Phacelia sp.*			*
LABIATAE	*Marrubium vulgare*			*
LOASACEAE	*Loasa bergii*	*		
ONAGRACEAE	*Camissonia dentata*	*	*	*
PLANTAGINACEAE	*Plantago patagonica*	*	*	*
POLIGONACEAE	*Poligonum stypticum*		*	
ROSACEAE	*Aphanes parodii*	*	*	
RUBIACEAE	*Galium sp.*	*		
	Rebulnium richardianum			*
UMBELLIFERAE	*Bowlesia incana*	*	*	*
URTICACEAE	*Parietaria debilis*	*		

Appendix 3: Programme instructions in GENSTAT language for randomisation tests. Data values are percent similarity (Kulcyznski's index). Values in the data matrix are arranged as explained in section 4.2.

```
scalar [v=6] ns "number of sites"
scalar x[1...ns],y[1...ns]
delete [redef=y] m
matrix [r=!p(x[1...ns]);c=!p(y[1...ns])] m
read m
"Guanacos vs.Sheep Overlap in Veg Groups: SUMMER”
77 66 71 59 63 60
67 78 74 60 70 79
69 63 76 70 65 67
79 60 72 93 82 81
87 71 66 76 90 80
67 82 71 54 71 76
print m

matrix [r=ns;c=ns] id
calc id=0
diag [r=ns] diagmat
calc diagmat=1
calc id=id+diagmat

scalar meandiag
calc meandiag=sum(id*m)/ns
print meandiag
vari [n=ns;v=1...ns] v1,v2
randomize [seed=383495] v2
```

```
scalar [v=500] nsim "number of simulations"
vari [n=nsim] savemean
scalar [v=0] isim

for [ntimes=nsim]
calc isim=isim+1
calc v2=v1
randomize [seed=0] v2

matrix [r=!p(x[#v2]);c=!p(y[1...ns])] m1
calc m1=submat(m)
calc savemean$[isim]=sum(id*m1)/ns
endfor

print meandiag
scalar simp
calc simp=sum(savemean.gt.meandiag)/nsim
print simp
```

<u>Appendix 4</u>: Plant species presence in the environment and in guanaco and sheep faeces by region.

		Presence in the Environment			**Presence in Diet**	
Evergreen Phanerophytes		*NE*	*SE*	*C*	Guanaco	Sheep
ANACARDEACEAE	*Schinus johnstonii*	*	*	*	x	x
ASTERACEAE	*Brachyclados megalanthus*	*		*	x	x
	Chuquiraga avellanedae	*	*	*	x	x
	Chuquiraga hystrix	*		*	x	x
	Nardophyllum obtusifolium		*	*	x	x
CHENOPODIACEAE	<u>*Atriplex lampa*</u>	*		*	x	x
VERBENACEAE	*Junelia aff alatocarpa*	*	*	*	x	x
ZYGOPHYLLACEAE	*Larrea divaricata*			*		
	Larrea nitida			*		
	Berberis heterophyla		*		x	x
	Colliguaya integerrima		*		x	x
Deciduous Phanerophytes						
ASTERACEAE	*Brachyclados licioides*		*			
	Cyclolepis genistoides	*	*	*	x	x
	Psila spartioides		*		x	x
EPHEDRACEAE	*Ephedra ochreata*	*	*	*	x	x
FABACEAE	*Prosopidastrum globosum*	*	*	*	x	x
	Prosopis alpataco	*	*	*	x	x
	Prosopis denudans	*	*	*	x	x
NICTAGINACEAE	*Bouganvillea spinosa*			*		x
OLEACEAE	*Menodora robusta*	*		*	x	x
RHAMNACEAE	*Colletia hystrix*		*			
	Condalia microphylla	*		*	x	x
SOLANACEAE	*Lycium spp.*	*	*	*	x	x
Chamaephytes						
ASTERACEAE	*Baccharis crispa*	*				
	Baccharis darwini	*	*	*	x	x
	Brachyclados caespitosus		*			
	Chuquiraga aurea	*	*		x	x
	Chuquiraga erinacea	*	*		x	x
	Nassauvia glomerulosa	*				
	Nassauvia ulicina	*	*		x	x
	Senecio mustersii			*	x	x
FRANKENIACEAE	*Frankenia patagonica*	*	*		x	x
ROSACEAE	*Acaena platyacantha*	*	*		x	x
	Tetraglochin caespitosum	*			x	x
UMBELLIFERAE	*Mulinum spinosum*	*	*	*	x	x
VERBENACEAE	*Acantholippia seriphioides*	*	*	*	x	x
	Junelia seriphioides			*		

Appendix 4: continuation

		Presence in the Environment			Presence in Diet	
Perennial Grasses and Graminoids		*NE*	*SE*	*C*	Guanaco	Sheep
CYPERACEAE	*Carex sp.*	*		*	x	x
	Eleocharis sp.	*			x	x
POACEAE	*Distichlis spp.*	*	*		x	x
	Festuca pallescens		*		x	
	Hordeum sp.	*	*	*	x	x
	Poa ligularis	*	*	*	x	x
	Sporobolus rigens	*	*	*	x	x
	Stipa chrisophylla		*	*	x	x
	Stipa longilumilis	*	*	*	x	x
	Stipa neaei	*	*	*	x	x
	Stipa pampeana	*	*	*	x	x
	Stipa speciosa	*	*	*	x	x
	Stipa tenuis	*	*	*	x	x
Perennial Forbs						
ASTERACEAE	*Baccharis melanopotamica*	*				
	Gamochaeta aff. stachidifolia	*	*		x	x
	Grindelia chiloensis			*	x	
	Perezia recurvata	*	*	*	x	x
	Psila tenela	*	*			
	Senecio gillesii	*	*		x	x
	Taraxacum officinale	*				
CALYCERACEAE	*Boopis anthemoides*	*	*	*		x
CARIOPHYLLACEAE	*Cerastium arvense*		*			
	Herniaria cinerea	*	*	*	x	x
	Aff. Paronychia sp.	*		*	x	x
	Spergula ramosa	*	*			
	Spergularia sp.	*	*			
FABACEAE	*Adesmia villosae*					x
	Astragalus moyanoii	*		*	x	x
	Hoffmansegia erecta			*	x	x
	Hoffmansegia trifoliata	*	*	*	x	x
IRIDACEAE	*Sisirinchium junceum*	*	*	*	x	x
POLEMONACEAE	*Gilia laciniata*	*	*	*	x	x
PORTULACACEAE	*Calandrina colchaguensis*	*		*	x	x
SANTALACEAE	*Arjona tuberosa*	*	*	*	x	x
SCHROPULARIACEAE	*Calceolaria sp.*	*		*	x	x
	Cardionema ramosissimmum	*	*		x	x
Annual Grasses						
POACEAE	*Bromus brevis*	*	*		x	x
	Bromus sp.		*	*	x	x
	Bromus trinii	*	*	*	x	x
	Schismus barbatus	*	*	*	x	x
	Vulpia spp.	*	*	*	x	x

Appendix 4: continuation

		Presence in the Environment			**Presence in Diet**	
Annual Forbs		*NE*	*SE*	*C*	Guanaco	Sheep
ASTERACEAE	*Duseniella patagonica*	*			x	x
	Facelis retusa	*	*	*	x	x
	Senecio chrysocomoides	*				x
BRASSICACEAE	*Lepidium mirianthum*	*	*		x	x
CARIOPHYLLACEAE	*Arenaria aff. Serpillifolia*		*			
	Cerastium junceum	*		*	x	x
	Spergula villosa		*	*	x	
CONVOLVULACEAE	*Dichondra microcalyx*	*			x	x
CRUCIFERAE	*Capsella bursapastoris*		*		x	x
	Draba australis	*	*	*	x	x
FABACEAE	*Adesmia smithii*	*	*		x	x
	Vicia pampicola	*	*		x	x
GERANIACEAE	*Erodium cicutarium*	*	*	*	x	x
HYDROPHYLLACEAE	*Phacelia sp.*			*		
LABIATAE	*Marrubium vulgare*			*		
LOASACEAE	*Loasa bergii*	*				
ONAGRACEAE	*Camissonia dentata*	*	*	*		x
PLANTAGINACEAE	*Plantago patagonica*	*	*	*	x	x
POLIGONACEAE	*Poligonum stypticum*		*			
ROSACEAE	*Aphanes parodii*	*	*		x	x
RUBIACEAE	*Galium sp.*	*				x
	Rebulnium richardianum			*	x	x
UMBELLIFERAE	*Bowlesia incana*	*	*	*	x	x
URTICACEAE	*Parietaria debilis*	*				

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