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POPULATION DYNAMICS AND SOCIOECOLOGY OF THE GUANACO (*Lama guanicoe*) OF MAGALLANES, CHILE

by

Kenneth John Raedeke

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

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(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree College of Forest Resources

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Signature Ken Raedeke

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CHAPTER 1

Introduction

1.1 Introduction

All animal species have the reproductive potential to increase in an infinite manner, yet none do. Biologists have long been intrigued by the factor(s) that limit the growth of populations. Numerous studies have concentrated on defining how environmental factors and biological characteristics of the population have interacted to determine the number of individuals of the different species in any particular community.

Malthus (1798) was the first to formally consider the interaction of reproductive potential of a population, and the factors that limit the growth of the population. He understood the factors that were limiting the population, and was concerned with the consequences of the limits on population growth. Charles Darwin considered the problems posed by Malthus, and incorporated the consequences of population regulation in the theory of natural selection. "He assumed that competition for the limited resources caused the regulation of numbers, thus not all offspring could survive to reproduce, and only the fittest would survive" (Tamarin 1978:2).

The mechanisms of population regulation have been vigorously debated by ecologists since the time of Malthus. Two major schools of thought have long dominated the discussion. The first school holds that populations are limited in a density-dependent fashion: as numbers increase, competition for resources intensifies, and population growth finally ceases. This school, often called the biotic school, is concerned with competition, predation, disease, and parasitism as mechanisms of population regulation. The other school holds that populations are limited by periodic changes in the abiotic factors of the environment, that reduce the population in a generally density-independent manner. The abiotic school is primarily concerned with weather as a regulating mechanism.

In recent years, a third, compromise, approach to the problem of population regulation has become more widely accepted. The compromise approach proposes that "a whole host of agents in the environment can regulate a population, and whether or not a population increases or decreases depends on the totality of these agents making the environment more or less optimal" (Tamarin 1978:93). Even though most population studies show regulation to be a compromise between the first schools of thought, the debate between the schools has not yet subsided. The acceptance of a compromise approach has been plagued by the problems of confounding terminology, the difficulty of generalizing from one organism to another, the difficulty of studying long-term phenomena, and the differences in the approach of theoretical, laboratory, and field biologists.

A complete review of the development and current status of the theories of population regulation is beyond the scope of this introduction. However, the historical development of the topic, and the benchmark papers on the subject have been complied and reviewed by Tamarin (1978). Other reviews of the current state of knowledge on population regulation are given by Hutchinson (1978), May (1976), and MacArthur (1972).

The present study has two principal topics: the first is the factors that are important in the regulation of ungulate populations, and second is the role of competition in partitioning the limited resources of ungulate habitat on sympatric range.

Unlike theoretical ecologists who often select the organism or ecological community for study that is most convenient for their particular problem or hypothesis, I have chosen the guanaco for study because of the precarious status of the species throughout most of its range. The status of the guanaco is precarious for three reasons. First, since the turn of the century, the guanaco has been eliminated from much of its former range, and has been reduced to semi-isolated small remnant populations in marginal habitats. The current population size is probably less than 1% of the aboriginal population. At the same time, the demands on the habitat are increasing, and the available range is continually reduced.

Second, unlike the vicuna which has a demonstrated economic value, and consequently has been the focus of intensive research and protection, there is little local, national, or international concern with the conservation problems of the guanaco. This is partially the result of a lack of information on the plight of the species. In much of Patagonia, the guanaco is still considered to be a pest, and has been given no effective protection from indiscriminate slaughter.

Third, until this study, there has been no systematic, long-term study of any aspect of the life history and ecology of the guanaco. Any attempts to manage or promote the protection of the guanaco have been thwarted by a lack of information on the plight and biological needs of the species.

1.2 Literature Review

Numerous general accounts of the life history of the guanaco have been written in natural history books and animal encyclopedias such as Lydekker (1896), Stassen (1916), Cabrera and Yepes (1940), Cornish (1917), and Walker (1963). These accounts are second hand, based on short term observations, hearsay, local myths, and Indian lore. Housse (1930) is a good example of how myths and legends can be incorporated into the scientific literature, and repeated in later accounts.

The best information available on the natural history of the guanaco comes from observations of early naturalists and explorers who traveled through South American on various expeditions. The earliest account is by Molina (1808), followed by Darwin (1845). Other early accounts of different aspects of the life hsitroy of the guanaco were reported by Allen (1905), Prichard (1902), Simpson (1934), and Link (1949). The life history of all the South American camels was summarized by Romero (1929), and Cardozo (1954).

An interesting account of the general habits of the guanaco and the local Indians that hunted the guanaco along the Beagle Canal was recorded in the autobiography of Bridges (1948), an early pioneer in the region. Gilmore (1950) described the relationship between the Indians of the interior and the guanaco as their main resource.

Many authors have contributed to our knowledge of the former distribution and abundance of the guanaco. An interesting early attempt to estimate the guanaco numbers in the southern Patagonian region was written by Rogers (1877) who based his estimate on Indian hunting patterns. Other valuable accounts were published by Darwin (1845), Osgood (1916 and 1943), Mann (1945 and 1953), Allen (1942), MacDonagh (1949), Gilmore (1951), and Pearson (1951). More recent accounts of current distribution and status are given by Dennler de la Tour (1954), Grimwood (1968), Howard (1969), Markham (1971), Miller *et al.* (1973), and Nuevo (1974).

Observations of guanacos in zoological gardens have produced a considerable amount of information on the life cycle of the guanaco. The reproductive ecology was studied by Brand (1963), Crandall (1965), Brown (1936), and Schmidt (1973). Benchley (1943) commented on the general habits of the species. Roig (1963) studied the nutrition and condition of various captive mammals, including the guanaco.

The taxonomic status of the guanaco and the Tylopoda in general has been discussed by Molina (1808) and Lonnberg (1913). More recently Bohlken (1960) studied the stomach morphology of the guanaco, and the relationship of the guanaco to the other members of the genus. Capurros and Silva (1960) did cromatographic studies on the generic relationships of the four South American camels. Cardozo

(1954), MacDonagh (1940) and Gray (1971) discussed the interbreeding of the four species of the camels. The evolution of the South American fauna in general has been studied by Hershkovitz (1969), Simpson (1950 and 1969), and Webb (1978), and reviewed by Cardozo (1975) with special reference to the lamoids.

Recent studies have concentrated almost exclusively on physiology and anatomy of the guanaco. The general physiology of the guanaco stomach has been studied by Vallenas (1970), Cummings *et al.* (1970), Vallenas and Stevens (1971a and 1971b), and Vallenas *et al.* (1971). The physiology of the kidney was studied by Rossenmann (1963). Thermoregulation by guanacos was studied by Rosenmann and Morrison (1963), and Morrison (1966). In all the above studies, the subjects were captive animals, and the sample sizes often consisted of a single individual.

Earlier studies of physiology and anatomy include Bullock (1929) who decribed the stomach stones, called "bezoars", Rusconi (1930) who described various dental abnormalities, and Hall (1937) who worked on the blood chemisitry of the lamoids.

While many authors have commented on the general behavioral patterns of the guanaco, only two have published accounts of any systematic studies. Rhors (1957) published general remarks on behavior and social groups, based on short term herd composition counts. Franklin (1975) conducted a one week study of the behavior of the guanacos in a small, remnant population in Peru.

The overall result of these various studies is a good understanding of guanaco distribution (both historical and current), general social organization, specialized physiology and anatomy, and taxonomic status. However, the guanaco population dynamics (especially the reproductive ecology), habitat requirements, population status, food habits, and relationship with the domestic stock are little known. Also, methodologies for the determination of sex and age nave not been described before the present study.

It has been the aim of the present investigation, in addition to addressing the general topics of population regulation and competition, to provide a more complete description of the entire life history of the guanaco of southern Patagonia.

1.3 The Scope of the Present Study

The present study was a segment of a continuing study of the fauna of Chile by the Chilean Corporacion Nacional Forestal (CONAF). The study was initiated in March 1972, and the field work continued through June 1975. The data analysis and laboratory studies have continued until December 1978.

The field work was generally confined to the province of Magallanes, with an intensive study area on Isla Grande. However, several surveys were made in the surrounding regions of Argentina. The Chilean government was particularly interested in the guanacos of Magallanes since they constitute approximately 95% of the guanacos remaining in Chile (Miller _et al_. 1973).

1.4 General Hypothesis

In the absence of significant predators, both guanacos and sheep are ultimately resources limited, and are in competition for the finite resources of the environment. Sympatric taxa will divide resources under the force of competition, resulting in such phenomena as character displacement or niche shifts, and ultimately speciation. Hence, competition results in natrual selection, and is essentially a density-dependent phenomenon, regulating populations through changes in population recruitment and mortality.

1.5 Purpose and Objectives

The purpose of this study was twofold, first to provide basic data on the life history, habits and ecology of the guanaco of southern South America, and second, to evalute the competitive relationships between free-living ungulates and their introduced domestic competitors. The guanaco-sheep interactions are of both theoretical and practical significance since the guanaco had no ungulate competitors until the introduction of the sheep. An understanding of the changes in population size and niche parameters including distribution and food habits, that were associated with competition, could help us understand competition and resource partitioning between other ungulate herbivores.

The specific objectives of this research were:

1. To inventory the distribution and abundance of the guanaco of southern Chile.
2. To determine the food habits and preferred forage plants of both the sheep and the guanaco.

3. To measure the parameters of population dynamics of both guanacos and sheep in order to determine the facor(s) that are controlling the growth of the populations.

4. To model the interspecific competition between the guanacos and the sheep.

5. To provide other life history information necessary in the development of conservation and management plans for the guanaco and its ecosystem.

CHAPTER 2

The Study Area

The intensive fieldwork was conducted on Isla Grande, the largest island in the Tierra del Fuego archipelago, located at the southern tip of South America. It is separated from the continent by the Straits of Magellan on the north and west, and is bounded by the Pacific Ocean on the west, the Atlantic ocean on the east, and the Beagle Canal on the south. The main study area roughly corresponds to the Estancia Cameron, in the Chilean sector of the Rio Grande river basin, just north of the interface of the forest and pampa grasslands. The location of the study area is given in Figure 1. An excellent summary of the climate, physiography, and vegetation of the island in general is given by Humphrey *et al.* (1970).

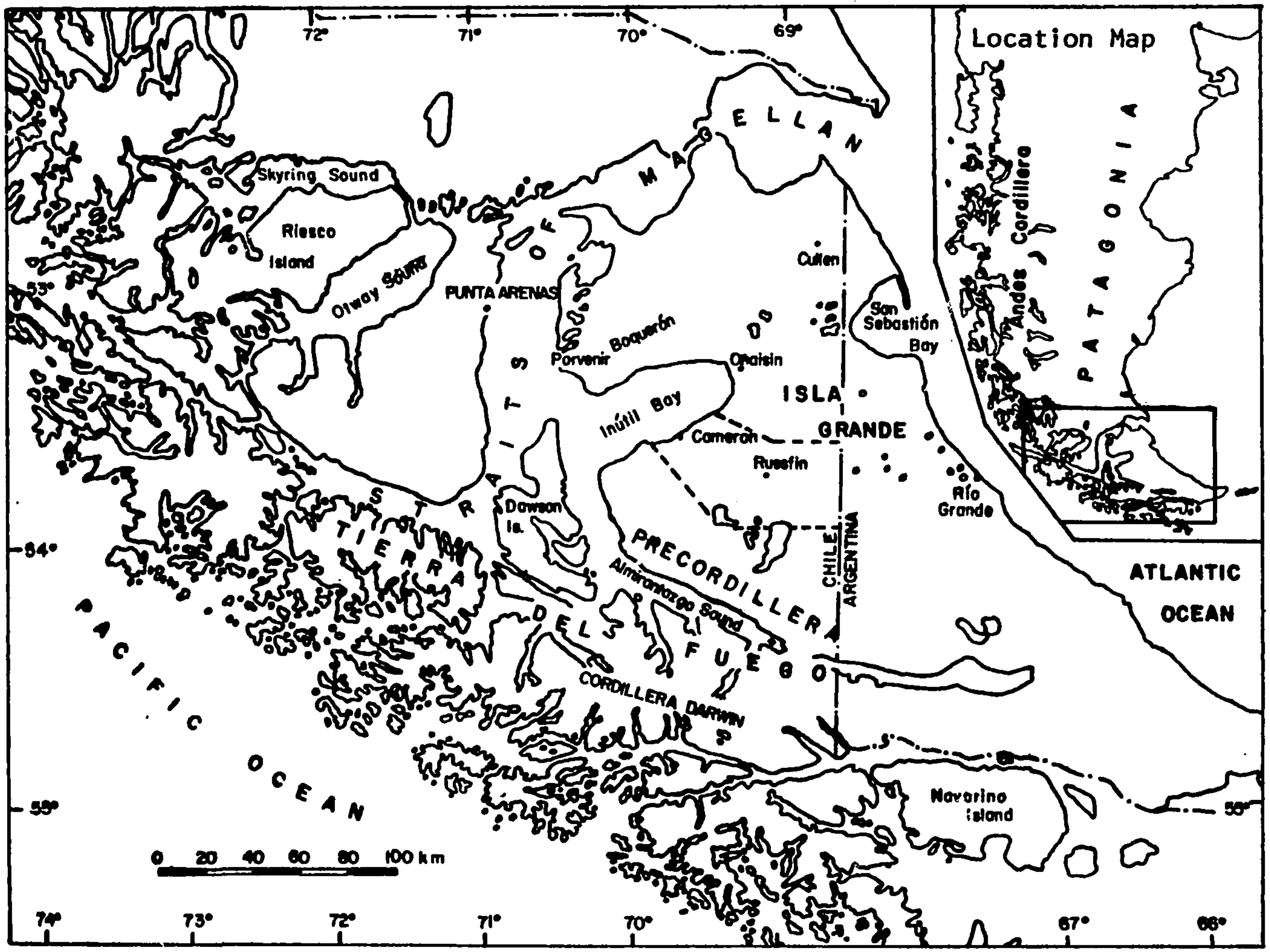


Figure 1. The location of the study area on Isla Grande, Tierra del Fuego.

2.1 Physiography of Isla Grande

Isla Grande is approximately 18,000 square miles in area, with all lands west of 68 degrees 36 minutes belonging to Chile, and the lands to the east belonging to Argentina. The island extends from 52 to 55 degrees south latitude, and from 65 to 72 degrees west longitude.

Three distinct landforms are found on the island: (1) the Andean Cordillera, running NW-SE along the southern part of the island, from 1,500 to 3,000 meters in elevation, and 50-60 kilometers in width; (2) the Precordillera, flanking the Andes on the north with elevations varying from 500 to 1500 meters, and 30-50 kilometers in width; (3) the pampas or lowland plains extending to the north of the precordillera to the Atlantic Ocean, varying in width from 10 to 350 kilometers.

2.1.1 The Andean Cordillera

The Andean Cordillera is a high, rugged range, with elevations of 3,000 meters. Glaciers occupy the peaks along most of the extent of Magallanes and Tierra del Fuego, coalescing into a continuous ice cap in the Cordillera Darwin of sowthwestern Isla Grande. The entire Cordillera has been sculptured by vast continental glaciations of the Pleistocene, and by the present alpine glaciations, with the outlet tongues eroding broad U-shaped valleys. Some valleys, now filled by the sea, form fiords and sounds that honeycomb the southern part of the island, while those valleys within the mountains most frequently hold bogs in their flat bottoms. The Cordillera is disected by many raging, glacier fed rivers and many parts are virtually inaccessable. Krank (1932) and Rudolph (1934) give excellent detailed descriptions of the geology and physiology of the Cordillera.

The Andean Cordillera provides little suitable habitat for the guanaco, and only the fringes of the area have been colonized. Throughout the Cordillera of the island, the land is barren and lifeless above 500 meters (Kuschel 1960). Above 800 meters, most of the Cordillera is covered by permanent snow and ice. Alpine meadows are almost completely absent due to the steepness of the terrain. Figure 2 shows the ruggedness of the main Cordillera, with the rolling hills of the precordillera in the foreground.

2.1.2 The Precordillera

The uplifting of the main Cordillera gradually dies out toward the north, and the precordilleran terrain is lower, and less rugged than the main cordillera (Figure 2). The precordillera was glaciated during the Pleistocene by piedmont glaciers flowing from source areas in the main cordillera. The glaciers scoured out large, broad valleys and basins, and left little depositional material. Through these valleys may be well drained, it is common to find big bogs or large lakes occupying the depressions, such as Lago Blanco, Lago Lynch, and Lago Chico on Isla Grande, and Lago Sarmiento in Argentina (Raedeke 1974). Dense woods and bogs occupy many of the valleys that are not filled by lakes.

The mountains of the precordillera attain a considerable height, especially in the highlands north of Seno Almirantazgo, with peaks reaching 800 to 1200 meters. However, sharp summits are lacking, and most peaks are mountain moorlands on the summit. Perpetual snow is found

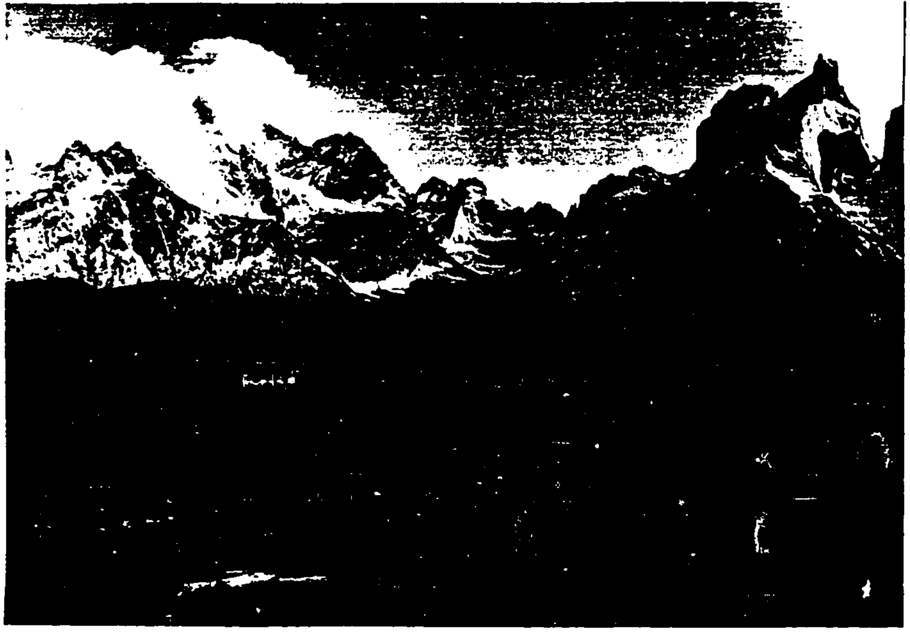


Figure 2. The Andes Cordillera with the rolling precordillera in the foreground.

Figure 3. The rolling Precordillera of Isla Grande, with the pampa in the foreground.

in sheltered areas in scattered patches on some of the summits (Krank 1932).

This zone has become an important area for the surviving guanacos of the island. The high mountain meadows and moorlands are frequently used as summer range by the guanacos which winter in the southern part of the study area. The tree covered lowlands provide winter cover and browse (Romero 1927, and Bridges 1948). This region is now only lightly utilized by sheep in the summer, and seldom used by sheep in the winter.

2.1.3 The Patagonian Pampas

The northern half of the island is typical of the extensive, open, wind swept pampas of southern Patagonia. The pampas are characterized by low, gently rolling plains, descending from the precordillera to the sea (Figure 4). The area is dissected by large rivers originating in the cordilleran glaciers, has many small streams, and is dotted with ponds, lagoons, and bogs.

The low topography of the plains is interupted by glacial features providing relief in the flat landscape. Huge end moraines frequently rise over 350 meters, marking

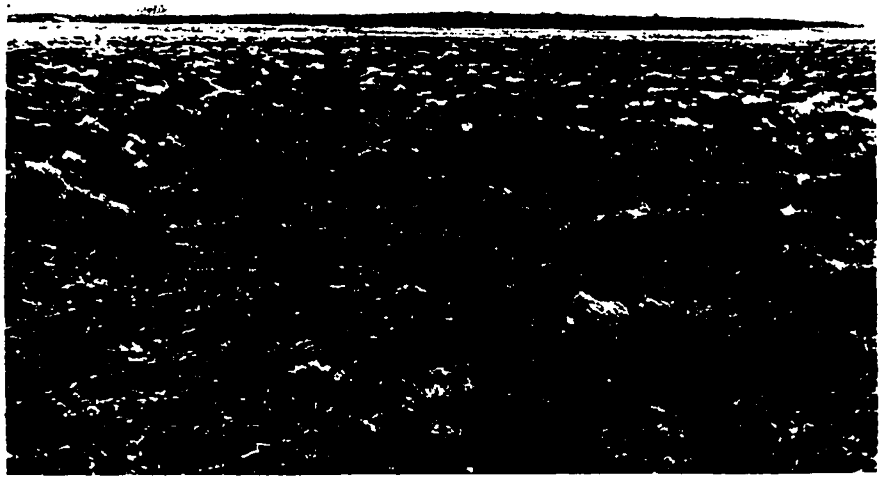


Figure 4. The Patagonian pampa at the foot of the precordillera, southern Isla Grande.

the termini of the Pleistocene glaciations. Numerous smaller moraines are also scattered about the pampa providing more local relief. The knoll and kettle topography mark sections where broad areas of glacial ice stagnated and melted during the retreat of the glaciers. Large outwash channels bisect the landscape, forming expansive terraces in the otherwise rolling pampas.

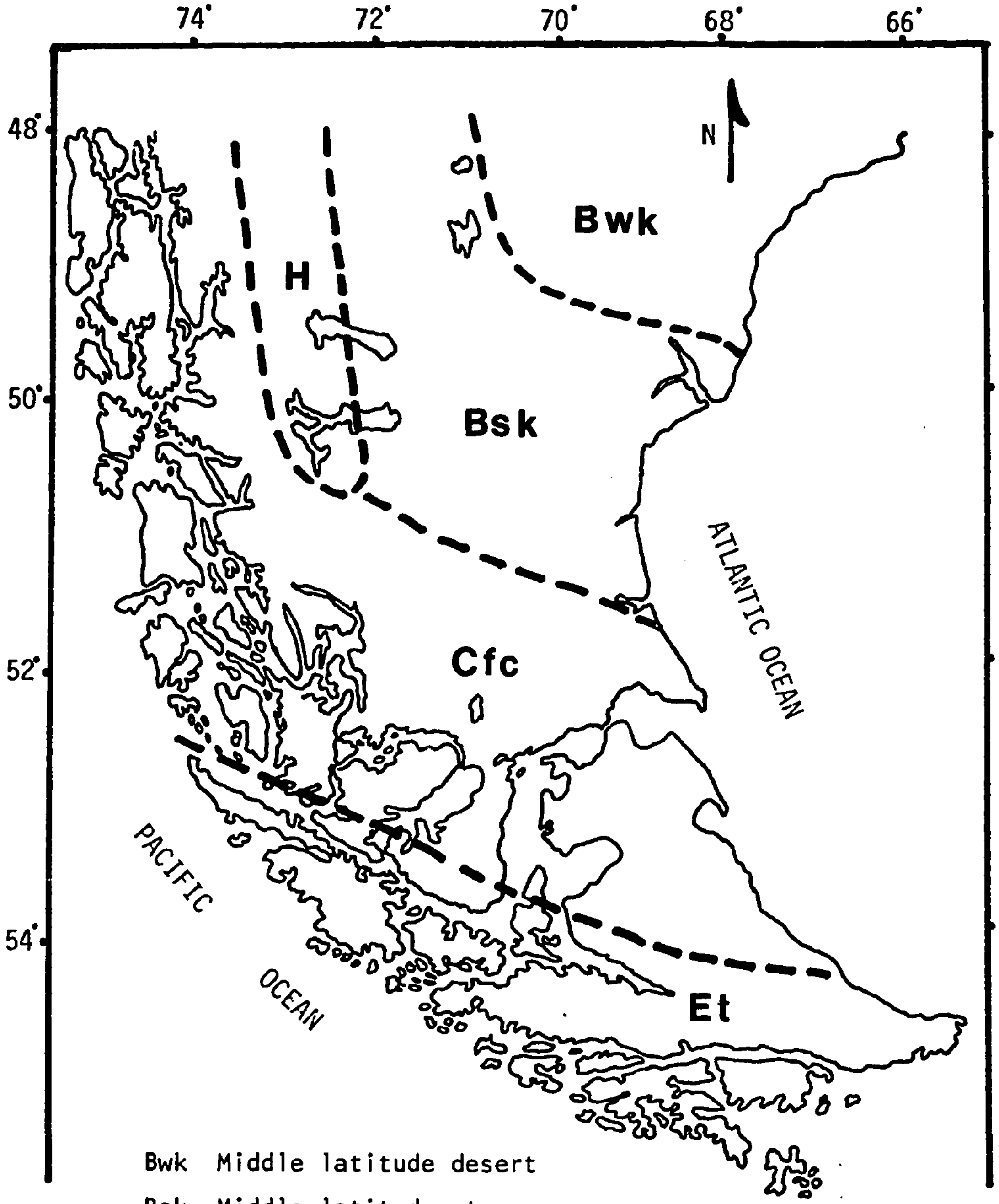
The pampa soils are characterized by poorly developed podsolic soil, prairie soil, and alpine meadow soil types (Diaz and Roberts 1960). Little or no soil development is found in the extensive gravelly glacial outwash areas, or in the areas of extreme eolian erosion.

2.2 Climate

Throughout the Patagonian region, the winters are long, wet, and cold, and the summers are short, dry, and cool. Within this framework, two climatic zones are described for Isla Grande: Temperate Continental (Cfc) in the northern pampas, and Tundra (ET) in the southern mountains. Much of the guanaco range in Argentina is located in the Cold Steppe (Bsk) climatic zone, which does not extend south into Chile (EDIT 1968). The greater part of the guanaco range in Isla Grande, and Magallanes in general, is located within the Cfc zone, and only this zone will be discussed. The climatic zones of the region are shown in Figure 5.

The Temperate Continental zone (Cfc) of the study region is characterized by the following:

1. Dry climate, with annual precipitation ranging from less than 500 mm to 1000 mm.
2. Cool the year round, with average annual temperature less than 10 degrees celsius, and the warmest average monthly temperature less than 15 degrees centigrade.
3. Seasonal variation in temperature is small, with



Bwk	Middle latitude desert
Bsk	Middle latitude steppe
Cfc	Temperate, no dry season, cool summers
Et	Tundra
H	Various local climates

Figure 5. The climatic zones of southern South America.

frost possible in any month, and precipitation falling in the form of snow, hail, or ice crystals throughout the year.

4. The precipitation is concentrated in the fall and early winter months.

5. The growing season is short, permitting herbaceous plants to mature and sustain a large number of herbivores.

6. Strong westerly winds occur in all the months, but are strongest in spring and summer.

Weather records for the study area are few. The data on weather patterns, presented in Table 1, are from the Cerro Guido station, located in the same climatic zone and in the same physiographic position as the study area. This table is based on a 39 year average.

A significant attribute of this climatic region is that the growing season is so short that food crops can be cultivated only on small plots with exceptionally favorable microclimates, which must be intensively farmed. Only alfalfa can be grown somewhat more extensively, and even this is low in productivity.

Snow accumulation patterns are an important factor influencing the seasonal distribution of both the sheep and guanacos on the island. In the interior of the island, snow accumulation occurs from June through August, making much of the range unsuitable as ungulate habitat, 'Table 1. Weather records for the Cerro Güido Station, Magallanes. The data are based on a 39 year record, from 191928-1967 (IREN 1967).

Month	Precipitation (in mm.)	Temperature °C		
		Average	Average max.	Average min.
Janurary	28.1	12.5	18.5	6.7
February	25.8	13.0	19.2	6.6
March	32.7	9.4	15.4	4.3
April	34.9	6.0	11.3	2.4
May	24.4	2.7	6.9	-0.7
June	19.0	0.5	3.4	-2.6
July	17.3	0.8	4.0	-2.3
August	16.2	1.2	5.0	-1.5
September	20.7	2.8	8.3	-1.5
October	17.1	8.4	14.8	2.3
November	20.8	9.9	16.2	3.4
December	20.2	12.2	19.4	5.5
Annual	277.2	6.6	11.9	1.9

since the snow is often crusted and reduces the availability of the grasses and other low growing forage. Heavy snow accumulation forces the guanacos and sheep to concentrate on the areas with reduced snow accumulation, thus reducing the carrying capacity of the winter ranges. Winter range with reduced snow accumulation, is the most limited range type. In the winter of 1972 the snowfall was considered to be normal, with depths measured to be

25-30 cm in August on the flat near Russfin. In the winter of 1973, the snowfall was early, and quite heavy, with depths measured to be 40-80 cm in July. Sheep and guanaco losses were extremely heavy throughout the region in the winter of 1973.

Annual precipitation on Isla Grande varies from over 2,000 mm in the southern mountains to less than 300 mm in the pampas, over a map distance of 150 kilometers, going from southwest to northeast (Pinto and Pino 1972). The greatest precipitation occurs on the west side of the Andes, which are buffeted by the westerly winds off the Pacific Ocean. The Andes create a rain shadow to the east of their crest, this rain shadow is the primary factor causing the formation of the arid grasslands and deserts of Patagonia. The annual precipitation to the east of the Andes is generally less than 500 cm. Throughout the region, the climate of the coastal zone is moderated by the surrounding ocean waters. Coastal areas are warmer in the winter and cooler in the summer. The average temperature at the Estancia Cameron headquarters located on the shores of Useless Bay is 6 to 10 degrees celsius warmer in the winter and 5 to 6 degrees celsius cooler in the summer than is Russfin, located 45 kilometers inland from Cameron. This results in less snow accumulation along the coastal areas, and a longer growing season, making the coastal zone preferred winter range for ungulates.

2.3 Flora

Due to the variety in landforms, elevation, and climatic conditions, the southern part of Patagonia has a diversity of vegetation. Within the region, Pisano (1973) has described eleven biotic provinces which can be generalized into five biotic or vegetational zones, as follows: alpine tundra, Magallanic moorland, evergreen beech forest, deciduous beech forest, and Patagonian steppe. The last two zones are the most important with regard to the distribution of the guanaco. Figure 6 shows the location and physical relationships between the vegetational zones. A detailed descriptions, of the vegetation of the region is available in Auer (1958), Kuschel (1960), Godley (1960), IREN (1967), Humphrey *et al.* (1970), and Pisano (1973 and 1974). The vegetation zones that are important for the guanaco will be described below.

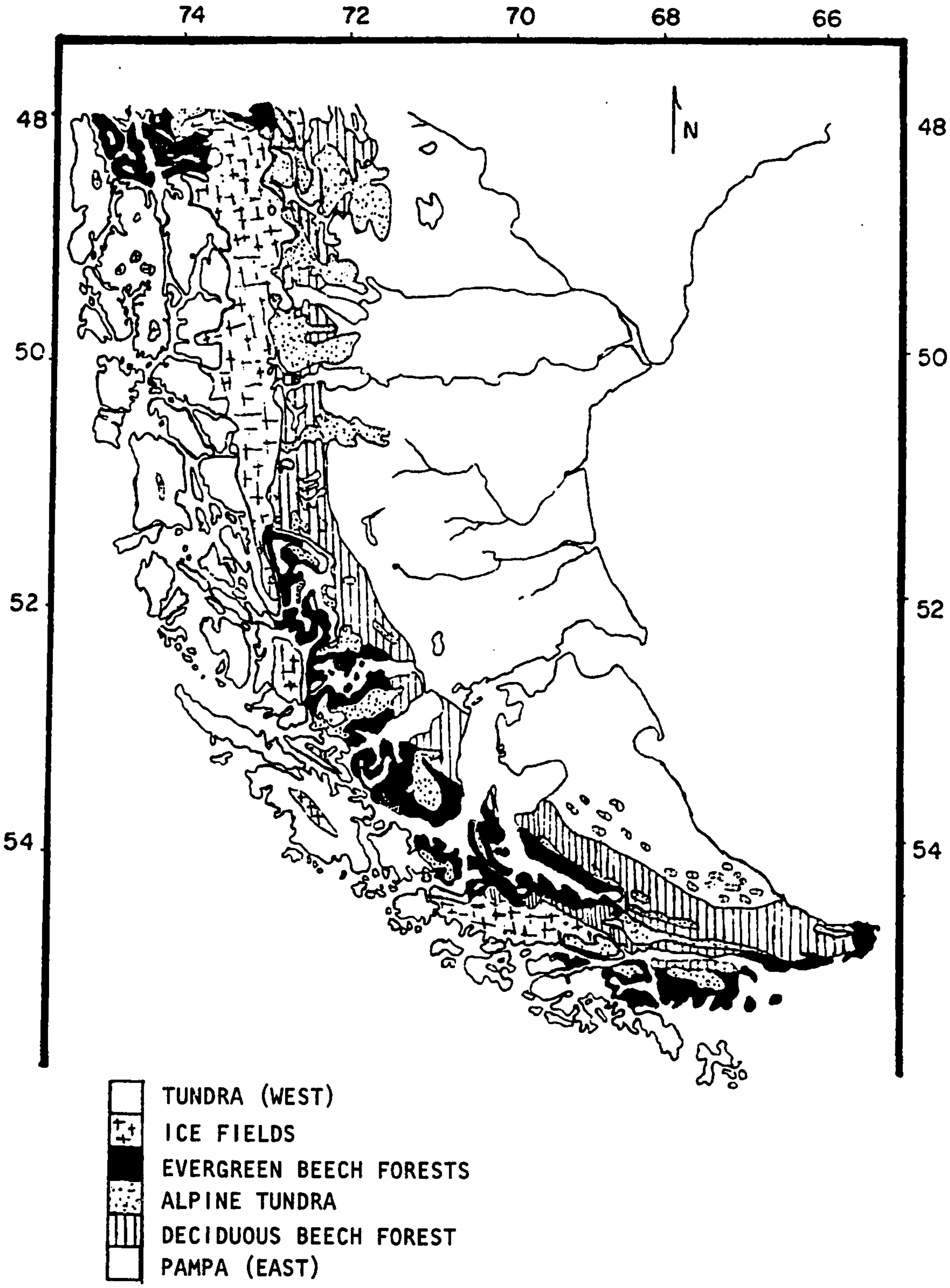


Figure 6. Vegetation map of southern South America. Adapted from Godley (1960).

2.3.1 Patagonian Steppe

This vegetation zone is the characteristic pampa grassland of southern South America, and is extensive in both Chile and Argentina, at elevations below 500 meters. Figure 7 shows the appearance of a typical scene in this vegetational zone, which comprises all the non-forested areas east of the Andes. The pampa grows drier with greater distance south and west of the precordillera. The rainfall in this zone varies from 200 to 500 mm per year. The vegetation is low xerophilous, and is dominated by spiny small shrubs, and hard bunch grasses (Kuschel 1960). Ground cover is incomplete and bare ground is found between the bunch grass clumps.

The grass species present are dominated by *Festuca gracillima* and *Festuca pallescens*. In the drier northern parts of the zone *Mulinum spinosum* is typical of the area, mixed with *Stipa* spp. All these grasses are locally called "coiron". In the wetter sites with well drained soils, especially the valley bottoms, the soft grasses such as *Deschampsia antarctica* and *Poa* spp. are found in abundance.

During the spring months, November and December, there is a moderate production of herbaceous plants on the pampas. The forbs produced during this period are valuable forage for guanacos and sheep while they are available.

Within this same grassland zone, large expanses of shrubs or "matoral" vegetation exist, especially on the wetter sites. With heavy sheep grazing pressures on the range grasses and forbs, these shrubs are now increasers on the range, since they are generally unpalatable to sheep. Figure 8 shows this vegetation association. The most common shrubs are low growing, about one to two meters in height. The most abundant species are romerillo *Chiliotrichium diffusum* and calafate *Berberis buxifolia*. In well developed stands, these shrubs are almost impenetrable. Many are spiny. Since these shrubs are not utilized by sheep, sheep ranchers have removed great expanses of these matoral associations mechanically removed, and reseeded with Australian, New Zealand, and North American grass species, in an attempt to increase the sheep carrying capacity of the range. These efforts were quite successful, especially on the wetter sites. However, with sustained heavy sheep grazing, the matoral vegetation is beginning to invade these improved pastures.

Figure 7. The Patagonian steppe vegetation type.

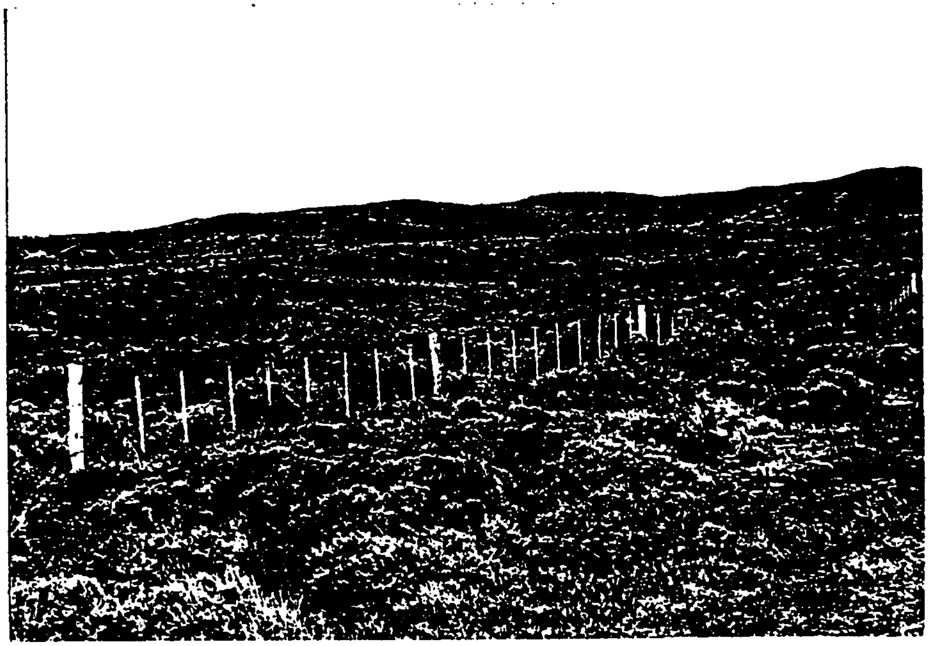


Figure 8. The matoral or shrub vegetation association within the grasslands vegetation type.

Interspersed in the pampa are large areas of acidic and poorly drained soil with a characteristic vegetation dominated by murtilla, Empetrum rubrum and various species of rushes. This vegetation association is very poor herbivore habitat, since these plants are not highly palatable to either the sheep or the guanacos.

2.3.2 Deciduous Beech Forest

The Magallanic beech forest found on Isla Grande is comprised of two principal forest types, whose distributions are related to rainfall, moisture, and temperature. The deciduous forest is found in the northern, warmer, drier parts of the forested portion of the island, while the evergreen forest is found in the southern, cooler, wetter parts of the forest zone. The relationship of these forest types to the steppe vegetation is shown in Figure 6.

The deciduous beech forest of the island is comprised of only two species of trees, lenga, Nothofagus pumilio and nirre, Nothofagus antarcticus. These two species are seldom found interspersed, but rather form pure stands (Figure 9 and 10). The lenga forest is most extensive, while the nirre forest is a transitional type between the open pampa and the lenga forest. The deciduous beech forest zone is bordered on the east and north by the grasslands, in the south by the evergreen beech forest, and at higher elevations by tundra.

Deciduous forests are found in the drier parts of the island, where precipitation varies from 400 to 600 mm annually. They are very open, with undergrowth limited to *Blechum penne-marina* a fern, and *Mesodendrum spp.*, a type of mistletoe.

The main shrubs in the understory are michay, *Berberis ilicifolia*, parrilla, *Ribes magallanicus*, and chaura, *Pernettya mucronata*. These shrubs are generally found in the more humid portions of this forest.

The herbaceous plant community of the forest floor is poorly developed. The more common plants are various species of *Ranunculus*, *Geum magallanicum*, *Acaena ovalifolia*, and the fern *Blechum penna-marina*.

Of the two deciduous forest types, lenga and nirre, only the nirre is an important habitat of the guanaco. Due to its low, twisted growth form, nirre is much more available as browse than the taller, heavy trunked lenga. Also, the canopy cover of the nirre is seldom closed, thus

Figure 9. The lenga (Nothofagus pumilio) beech forest of Isla Grande.

Figure 10. The nirre (Nothofagus antarcticus) beech forest of Isla Grande.

allowing a greater development of the forest floor community.

2.3.3 The Evergreen Beech Forest

This forest type grows in the more humid portions of the island where precipitation varies from a minimum of 600 mm to over 2,000 mm annually. The evergreen forest is found to the south of the deciduous forest and to the north of the moorlands of the highlands. At higher elevations this forest is replaced by the tundra or moorlands.

There are three main tree species found in this forest, given in order of dominance: coigue, *Nothofagus betuloides*; canelo, *Drimys winteri*; and lenga. In the wetter areas, canelo becomes more abundant. Associated with these trees are the shrubs michey, murtilla, chaura, and chilco, *Fuchsia magellanica* (Pisano 1973). Ferns are also very common, especially the genus *Hymenophyllum*. Areas of poor soil drainage support large sphagnum bogs.

In all parts of this vegetation zone, the understory is well developed. In the wetter portions, to the south, the forest becomes almost impenetrable by man.

This vegetation zone is poor habitat for herbivores, and the faunal community is impoverished both in the number of animal species present, and in total biomass. It is used by the guanaco only along the fringes, especially along the eastern end of the Beagle Cannal where Bridges (1948) observed moderate numbers of guanacos in the fringes of the forest.

Interspersed in the forest communities, both the deciduous and evergreen, are the true sphagnum bogs. These are composed principally of *Sphagnum magellanicum*, and various grass-likes, such as the rushes *Marsippospermum grandeflorum*, and *Schoenus antarcticus*.

2.3.4 The Alpine Tundra

The alpine tundra lies above the treeline, and below the snowline. The soil is very dry, permiable, and rocky. The ground cover is very incomplete, made up of poorly developed, isolated shrubs, cushion plants (*Azorella* and *Bloax* genera), *Emperetum rubrum*, *Senecio*, and *Nassuvia*, and a few graminia (*Poa*, *Festuca*, and *Stipa*) forming poorly developed tussocks. Between the plants are only bare rocks and rocky soil.

The total plant productivity is low, but sufficient plant material grows to support a low to moderate number of guanacos during the summer months. The area is not used by domestic cattle or sheep.

2.4 Land Tenure Patterns

Chilean settlement of the province of Magallanes began in 1843 with the construction of Fort Bulnes. The first permanent settlement was moved to the present site of Punta Arenas when it was determined that cattle and sheep thrived on the pampas surrounding that area. However, in 1855 there were still only 34 sheep near the settlement.

Fullscale agricultural development began in the 1880's when the government auctioned off the first grazing rights to the land. The initial rights were leased for a period of from 10 to 20 years, with the option to renew if certain improvments were made. The first fences were constructed in 1883. In 1893 the first actual sales of land began. At this time the large "agricultural societies" were formed on the pattern of modern day corporations. These organizations bought land in large blocks, and established the famous estancias of the region. Many of the original stocknolder, managers, and settlers were British.

In 1910 two of the largest societies merged to form the "Ganadera de Tierra del Fuego". This large society controlled over 2,900,000 hectares in Magallanes by 1910. By 1928, the Society stabilized its holdings at approximately 1,900,000 hectares, which was more than all the other landholders combined, and included the best lands of the region. At this time this company controlled almost all of the grazing land on Isla Grande in Chile. However, of this total, 1,176,00 hectares were leased from the government. The total stock holdings of the Society in Magallanes province were 1,500,000 sheep, 6,000 cattle, and 10,000 horses (Erasmo 1972).

From the late 1930's to 1960 the government gradually recoverd the lands that had been leased to these large companies. These lands were then subdivided into smaller estancias, and leased to individuals. Little of the land was actually sold outright after 1900. By 1959, the Ganadera de Tierra del Fuego had relinquished all its leased lands, and its total holdings were reduced to 980,000 hectares. Even still, for Chile in general, in the late 1950's 1.5% of the landowners controlled 70% of the usable agricultural land (IREN 1967).

In 1967 the agrarian reform law was passed by the Chilean congress, allowing the government to expropriate abandoned or "poorly developed" lands, plus any owned by a single owner in excess of a certain amount. The purpose of the law was to increase the number of family farms, and to increase productivity. In 1969 the first lands were expropriated in Magallanes. These lands were subsequently managed in various ways, from cooperatives to individually leased plots to large communal farms. However, no land was sold to private individuals. The Ganadera de Tierra del Fuego lost over 50% of its productive capacity in 1969-1970 (Erasmo 1972). With the election of the Allende government in 1970, the remaining lands owned by the large societies in Magallanes were expropriated, and put into state owned communal farms, managed by worker committees.

After the military coup in 1973 the land ownership policies of the government changed dramatically. The new policy was to place the agricultural industry in the private sector. In 1978 the large communal farms were being subdivided, and sold to private individuals. The smaller farms that were previously leased are now being sold to the former renters. The largest farms of the region are now about 20,000 hectares.

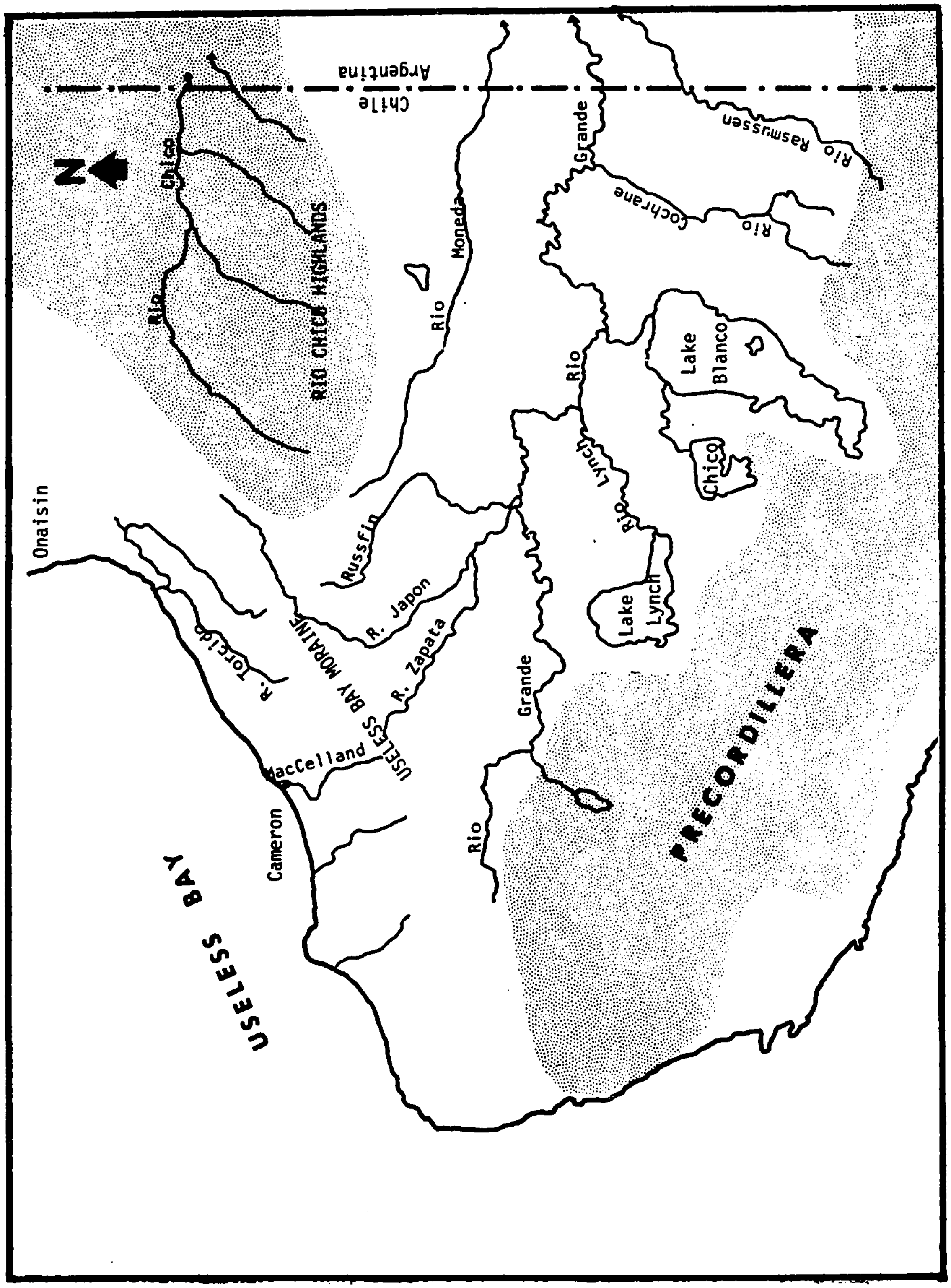
Sheep ranching is still the single most important sector of the provincial economy. In 1965 the province contained 2,979,272 sheep, 46,290 cattle, and 14,512 horses (IREN 1967), and agricultural exportations were valued at US $6,685,302. In the same year, Magallanes contained 41% of the sheep of Chile, and agriculture employed 17% of the work force of the province (IREN 1967).

2.5 The Intensive Study Area

The intensive field studies were conducted largely on the Estancia Cameron in the central portion of Isla Grande, from the north slopes of the precordillera to the rolling pampas. The study area was chosen because it has the highest density of guanacos in Chile, and probably in all of South America. Figure 11 shows the different land forms and river systems within the area.

The study area delimited in Figure 1 contained all the habitats and vegetation types of the island, with the exception of the wet moorlands and the high cordillera. Figure 12 gives a diagramatic crossection of the physiography and vegetation of the area along a line running north-south parallel to the international border

Figure 11. Physiography of the study area on Isla Grande, Chile.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Lake Lynch
Russfin
R. Japon
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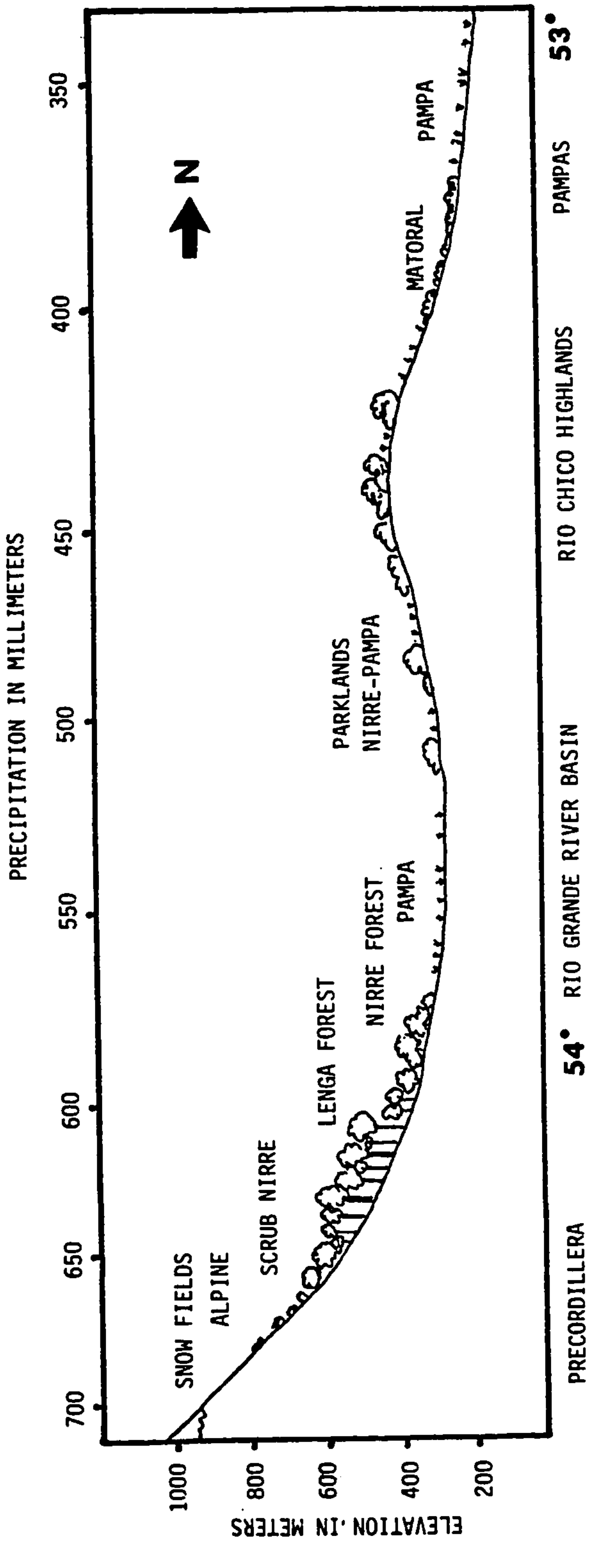

Figure 12. A diagramatic crossection of the study area. The section runs north-south across the Rio Grande Basin.

from 54 degrees 30 minutes to 53 degrees south latitude. The map in the back pouch shows the location of the settlements, fences, roads, rivers, and forests of the area. This map was compiled from forest type maps of IREN (1967), aerial photos, and other maps. The area of the estancia was approximately 200,000 hectares in 1975, 75% pampa steppe, and 25% forested. The forest was 16% lenga, and 9% nirre, with only a little evergreen forest. The nirre forest was generally found in small patches interspersed in the pampa, forming a parklands vegetation type, which covers about 30% of the estancia. The parklands association is shown in Figure 13.

Within the pampa grassland there are large expanses of matoral shrubs, sphagnum bogs, and rush meadows, so that probably less than 50% of the total estancia is in the grasslands or bunch-grass pampa type.

The topography of the study area is generally rolling, with little rapid change in elevation. Going inland from the headquaters on the coast, the elevation rises steadily to 350 meters in a distance of 25 kilometers. After this rise to the top of the Useless Bay moraine, the area is plateau like, with the Rio Grande basin draining to the east. Within the basin the elevation varies from 300 to 400 meters. There are

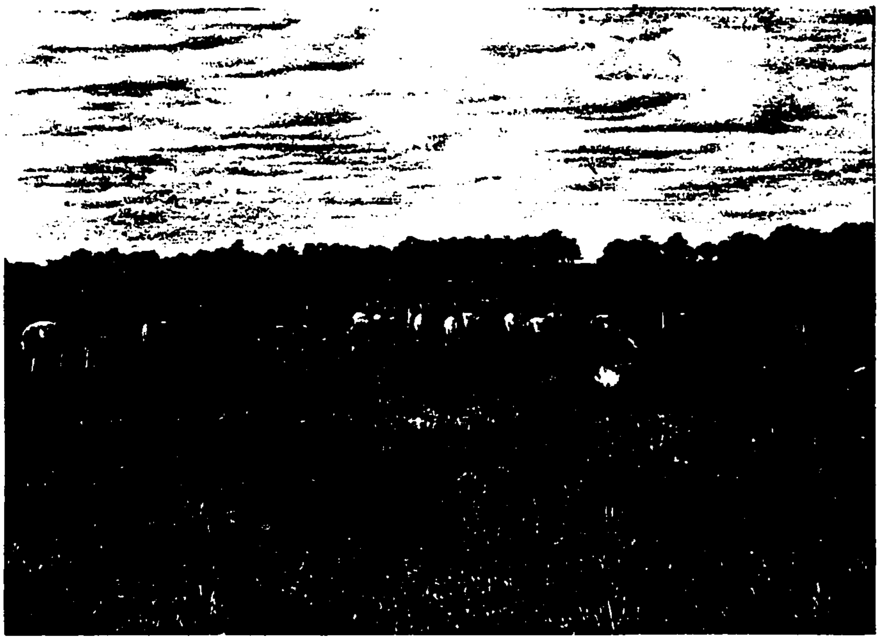

Figure 13. A group of male guanacos in the parklands vegetation association.

highlands both on the north and the south of the basin. These areas are covered with nirre forests, and are used as sheep summer range. The main sheep winter range is along the shores of the Useless Bay, west of the crest of the moraine, and in the northeastern sector of the basin.

The entire study area was grazed by sheep and other stock during at least part of the year. In January, the estancia maintained approximately 130,000 sheep, and herds of 1,200 cattle, and 600 horses. The sheep were grazed on the range using a rotational grazing system. The range was divided into summer and winter ranges, which were further subdivided into pastures. These pastures were grazed in regular succession through the grazing season. This type of range use is based on the assumption that a large number of grazers will make more uniform use of the forage (Stoddart *et al.* 1975).

Most of the pampa and basin region was accessible by four-wheel drive vehicle. However, the precordillera and the forested areas were penetrable only in limited areas where logging or petroleum exploration activities were in progress.

CHAPTER 3

Methodology

3.1 Distribution, Movements, and Behavior

Seasonal distribution, movements, and behavior were monitored through daily observations of guanacos and their sign throughout the study area during the entire year. Methods included systematic aerial and terrestial surveys. The aerial surveys were flown in fixed-wing small aircraft at low altitudes. A minimum of two surveys were flown annually: one in mid-winter, July or August; and a second in late summer, in February or March. Terrestial surveys were conducted throughout the year. Observations were made with the aid of 9X36 binoculars and a 15-45X spotting scope. All guanaco observations were recorded on vegetation and topographic maps.

The distribution of guanaco sign, especially fecal material, was used to determine distribution and seasonal use. However, since guanacos defecate in communal piles, fecal transects were used only to indicate presence or absence of guanacos, not population density.

Attempts were made to tag guanacos for use in the study of movements and behavior. Hand capturing of new-born was feasible, but subsequent observations indicated a very high mortality of tagged young, so this method was discontinued. Immobilization with Pneu-darts and Sucostrin was successful in trials with captive animals (Raedeke 1976). However, field attempts were unsuccessful.

Daily movements and behavioral patterns were studied through intensive observations of tagged and naturally marked animals within coherent social groups. These observations were made from a distance with the aid of binoculars, in order to not interfere with normal behavioral patterns.

3.2 Growth and Condition

Data for the analysis of growth and condition were collected from three sources: free-ranging guanacos collected during the study, animals found dead from natural causes, and animals captured alive. Whenever possible the following measurements were taken: total weight, carcass weight, organ and systems weights, total length (tip of nose to base of tail along the contour of the body), hind foot length (heel to the point of the hoof), tail length, ear length, chest girth (circumference of the chest immediately posterior to the shoulders), height at shoulder, and the length of the lower jaw (from mental foramen to the posterior corner of the jaw articulating surface, see Figure 14).

Physical condition was measured by the kidney fat index (Riney 1955), length-weight ratios (Taber 1956a), and bone marrow analysis (Cheatum 1949).

To calculate the kidney fat index, the weight of the kidney fat is divided by the weight of the kidney without the fat. The amount of surrounding fat included in the measurement is standardized by trimming the fat from the ends of the kidney perpendicular to the long axis of the kidney, tangential to each end (Riney 1955). The weight

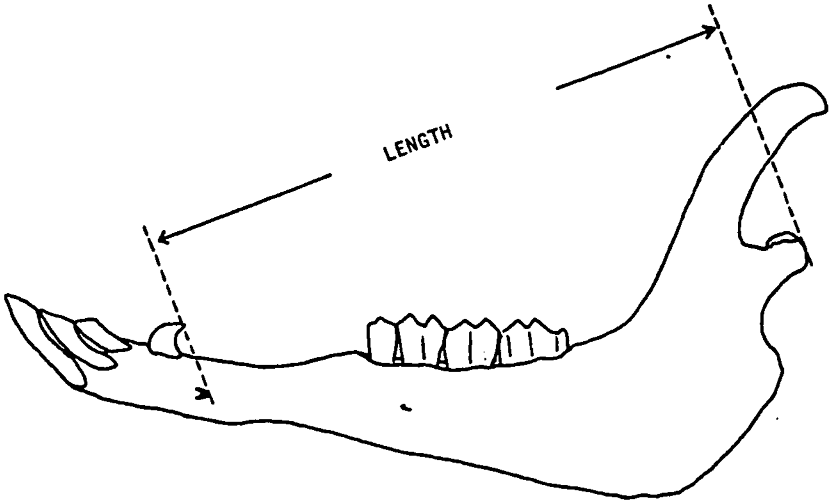

Figure 14. The method of measuring the length of the lower jaw.

of the kidney and kidney fat was measured with a spring balance scale to the nearest gram.

The growth of the eye lens was based on the wet weight of the lens from guanacos collected in the study. The eyes were removed immediately after the animal was sacrificed, and preserved in 10% formalin for 14 to 17 days. Both lenses were then removed, and weighed on a Mettler analytical balance.

3.3 Reproduction

The reproductive ecology of the guanaco was determined through the analysis of reproductive tracts collected from free-ranging guanacos, microscopic analysis of ovaries, observations of changes in population structure during the parturition season, field necropsies of natural mortalities, and the observation of breeding and reproductive ecology of captive and free-ranging animals.

An attempt was made to collect a representative sample of females from all age classes throughout the year. In the process of the autopsy, the presence or absence of a fetus, condition of the fetus, number of corpora lutea, evidence of resorbtion or abortion, and the condition of the mammary glands was recorded. In the early stages of pregancy, the entire reproductive tract was preserved in 10% formalin, and in the later stages, only the ovaries were preserved. All standard measurmements were recorded for both the fetus and the female.

The ovaries collected were sectioned, mounted and stained by a commercial laboratory for examination of the ovarian structures. The ovaries were first dehydrated, cleared, mounted in paraplast, and cut into 1.5 mm thick block. A permanent microscopic section was cut from each block and mounted. With the aid of a 40-100x microscope, the number and development of the ovarian structures such as the corpora lutea, corpora albicantia, accessory corpora lutea, regressing corpora lutea, and graffian follicals was determined. The identification of the ovarian structures was based on the work by San Martin *et al.* (1960), and Palominao and Torres (1968) who described the physiology of the ovary of the alpaca *Lama pacos*.

Field necropsies of guanacos dying from natural causes yielded further information on ovulation rates, resorbtion of embryos, and general reproduction. The reproductive tracts of all carcasses were throughly examined, and the same data was recorded as from females collected. Special attention was given to the condition of the female, and any indication of abortion or resorbtion of the embryo.

The observation of herd compostion changes during the season of parturition yielded several sorts of information: season of birth, parturition rates, and neo-natal mortality. The methods employed are described in the section on herd composition counts.

3.4 Mortality

During the study, every guanaco carcass encountered was classified when possible with regard to age, sex, cause of death, date of death, and location. Systematic searches were regularly conducted in areas where guanaco carcasses were most likely to be found, especially on key winter range. Field necropsies were performed on all carcasses to determine physical condition, cause of death, parasite loads, and other debilitating conditions.

Neo-natal mortality was estimated through the observation of the female-chulengo ratios throughout the year, and especially in the post-parturition period.

Guanaco remains were sexed on the basis of pelvic bones (Taber 1957a) and the size of the canine teeth. Male lamoids have canine teeth that are much larger than those in females (Cabrera and Yepes 1940, and Koford 1957). When the age of the individual is taken into consideration, there is no overlap in size of canines between the sexes.

Upon initiation of this study, there was no published method for determining the age of individual guanacos, or of any South American lamoid. In the course of the study, three methods were developed to determine the age of any individual, based on dentition. Tooth replacement was used for individuals less than 3 years old, and annuli in the tooth cementum and also tooth wear were used for individuals over three years old. A detailed description of these methods is given in Appendix A.

3.5 Herd Composition

Population structure was determined by observing and classifying undisturbed guanacos from a distance. Counts were made periodically throughout the year. However, the best period of the year was during the parturition and breeding seasons (December through March), when behavioral characteristics that were critical for differentiating sex and age classes were most pronounced.

Most observations were made during the mid-day when the animals were most visible as they foraged on the open pampa. Binoculars were necessary for most classifications, and a 15-45X spotting scope was often needed to confirm age classes.

The guanacos were classified into five different classes: adult males, yearling males (12 to 23 months old), adult females, yearling females, and chulengos (young of the year, less than 12 months of age). Since the wild lamoids are not sexually dimorphic in physical appearance, it is difficult to sex them in the field, except by behavioral characteristics. Whenever possible, however, sex was verified by observing the genital organs when the guanaco was defecating, urinating, dusting, jumping fences, or when the tail was raised during social interactions. Table 2 shows some of the characteristics by which these classes can be distinguished.

3.6 Abundance

The density of guanacos in the study area was estimated using the line transect method described by Gates et al. (1968). With this method, the population size "N" was estimated by traveling a distance "L" across a tract of land with area "A" in non-overlapping and non-intersecting transect lines. The number of animals sighted "n" was recorded together with the right angle distance "X" from the animal to the transect at the time of first sighting. One advantage of this method is that the density estimates can be calculated on the basis of

Table 2. The criteria for distinguishing sex and age classes of guanacos in the field.

Character	Adult Male	Yearling Male	Adult Female	Yearling Female	Chulengos
Body size	Large body	Smaller than adults	Large body	Smaller than adults	Smaller than all others
Pelage		Darker face		Darker face	lighter colored on head and body longer hair
Head shape	Long muzzle, flat headed	Slight bowl shaped face	long muzzle, flat face	Slight bowl shaped face	High crowned, short, blunt muzzle
Reproductive status			Often with with young	Never has young at side	
Behavior	Non-family males found in all-male groups Family group male aggressive toward males, observers, etc. Gives alarm	Found in all-male groups, playful	Usually in family groups, leads in escape flight	More playful than adult females	Follows mother, most playful of those in family groups

several different probability of sighting distributions, depending on the nature of the distribution patterns of the animals.

One assumption of this method is that the transects are located randomly throughout the sample area. This proved to be impractical, therefore the systematic road network of the study area was used as the sampling framework. Caughley (1977) argued that while the precision of random sampling is greater, systematic sampling is frequently more efficient.

All censusing was conducted at times when the guanacos were most observable, between 1000 and 1600 hours, on days without strong winds, rain, sleet, snow, or fog. Due to the great variability in observability of guanacos beyond 600 meters, only those animals observed at distances less than 500 meters from the transect were included in the results of the censuses from 1972 to 1975. In 1977 all guanacos sighted were included in the the sample.

An initial attempt was made to stratify the census area on the basis of vegetation, but since the area is characterized by small forests interspersed with pampa, the forest edge area is not clearly definable. This made it difficult to assign the animals to any particular plant community. Hence it was impossible to stratify on the basis of vegetation.

3.7 Food Habits

The composition of the diets of sheep and guanacos was determined by two methods: first, the diets of sympatric guanacos and sheep were determined by an analysis of the fecal material collected monthly from both species; and second, for the guanaco, the general diet was determined through analysis of rumen contents from guanacos collected systematically in all seasons throughout the study period.

3.7.1 Fecal Analysis

A composited sample of freshly dropped fecal material was collected from both sheep and guanacos occupying sympatric range. The fecal samples were collected from the area 10 kilometers north of Rio Grande. The area was yearlong habitat for guanacos, and winter range for sheep, although sheep were present in small numbers during the summer also. The samples were collected from June 1976 to June 1978. The composited sample consisted of 5 pellets from 20 different piles each for sheep and guanacos. Anthony and Smith (1974) reported that a composited sample of 15 sub-samples was sufficient to describe the seasonal diet for deer.

Standardized procedures were used to prepare and analyze the fecal material. Microscopic slides of the fecal material were prepared and analyzed using the method of Sparks and Malechek (1968), Flinder and Hansen (1972), and Hansen et al. (1977).

The procedure was as follows: after drying for 24 hours at 50 degrees C, the composited pellet sample was ground in a Willey mill through a 1.0 mm screen. A teaspoon of the ground material was mixed in hot water (approximately 42 degrees C) for one minute in a Waring blender to randomly mix fragments of similar size for proper sub-sampling. The sample was then bleached for 1 minute in a common household bleach, rinsed in water, and mounted on the microscope slide using Karo syrup. The amount of material on the slide was measured such that each field of view at 100 power contained approximately three discernable fragments.

An experienced biologist identified and quantified the plant fragments in the feces. Fecal fragments were classified into the catagories of grass, grass-like, browse, and forbs. The fields on each slide were viewed under a 100X binocular microscope. Five slides per fecal sample, and 10 fields per slide were analyzed, for a total of 50 fields per sample. Frequency of occurance of recognizable plant fragments were tallied for each sample. Frequency was converted to particle density per slide by using the Fracken and Brischle (1944) table. The percent relative density (%Rd), (the particle density of the forage type divided by the total number of particles of all forage types), was calculated for each forage type (Curtis and McIntosh 1950).

3.7.2 Rumen Analysis

The analysis of the rumen samples followed the methods described by Nellis (1962) and used by the Wildlife Laboratory, Montana State University. A one liter sample of rumen material was collected from each guanaco sampled. The samples were preserved in 10% formalin until analyzed. To separate the plant fragments the rumen sample was washed with fresh water for several minutes over a gang of sieves. Material that remained on the 6.35 sieve was saved. This plant material from the sieve was separated by species, and identifed by comparison to a reference plant collection. The reference collection, and all forbs, grasses and other questionable material in the sample was identified by Edmundo Pisano, plant ecologist of the Instituto de la Patagonia, Punta Arenas, Chile. A binocular microscope was used as necessary. The amount of each plant species separated in the rumen analysis was determined by volumetric displacement. All averages were calculated by the aggregate percentage method of Martin _et al_. (1946).

CHAPTER 4

The Guanaco Population

4.1 Taxonomy of the Guanaco

The guanaco, *Lama guanicoe*, is a member of the family Camelidae, which is the only family in the suborder Tylopoda. There are four species of the Camelidae in South America: the llama, *Lama glama*; the alpaca, *Lama pacos*; the vicuna, *Vicugna vicugna*; and the guanaco. The first two species are found only as domesticated species, and are generally thought to have descended from the guanaco (Fallet 1961). However, Capurros and Silva (1960) concluded that the alpaca is most closely related to the vicuna, and not the guanaco. They based their conclusions on chromatography and electrophoresis. At present it appears that the phylogenetic relationships of the four species are still uncertain.

The first description of the guanaco was given by Molina (1782), who called it *Camelus huanacus*. Waterhouse (1839) called it *Auchenia lama*, and the common name auchenia is still used to refer to all four lamoid species. The genus was named *Lama* by Frisch in 1775, and Mueller in 1776 called the species *Camelus guanicoe*. Thus the valid name of the guanaco is *Lama guanicoe* Mueller (Dennler de la Tour 1954).

Little work has been done on the taxonomy of the possible races or subspecies of the guanaco. Lonnberg (1913) described two subspecies for the guanaco mainly on the basis of skull measurements. These two subspecies are *Lama guanicoe cacsilensis*, the small guanaco of the area around Nunoa, Peru, and *lama guanicoe guanicoe*, a larger animal, for the rest of the range of South America. While these subspecies designations are still in common usage (Grimwood 1968, Cabrera and Yepes 1940, and Krumbiegel 1944) the subspecies described by Lonnberg for the Nunoa area has not been verified by later collections. Indeed, Osgood (1916) and Allen (1942) questioned the validity of this subspecies, since Osgood (1916:201) states that the specimens he collected in the same region "are not closely related to the 'small Peruvian guanaco' to which Lonnberg has given the name _Lama glama cacsiloensis_ (sic _Lama huanachus cacsilensis_) and which shows great similarity, at least in certain cranial characters, to the vicugna".

More recently, Krumbiegel (1944) described four subspecies of guanacos on the basis of crainal measurements of Lonnberg (1913), Osgood (1916), material from other collections, and his own samples. His classification is the following:

1. _Lama guanicoe guanicoe_ Muller 1776 found in Patagonia, Tierra del Fuego and Argentina south of 35 degrees south latitude.
2. _Lama guanicoe huanacus_ Molina 1782 found in Chile.
3. _Lama guanicoe cacsilensis_ Lonnberg 1913 found in southern Peru and Bolivia.
4. _Lama guanicoe voglii_ Krumbiegel 1943 found in Argentina, north of 32 degrees south latitude.

It has further been suggested (Bridges 1948) that the guanaco of Isla Grande is a separate subspecies from that of the mainland. This is based on comments that the island species is darker in color and larger in overall size than the mainland form. However, no such differences have been substantiated to date.

4.2 Historic Guanaco Populations

Ther are four distinct periods in the history of the guanaco populations: the Pre-Indian period; the Indian period; the Western colonization period; and the Post-colonization period. In each period the distribution and abundance of the guanaco was influenced by very different factors. The purpose of this section is to identify these different factors for each period, and to describe the status of the guanaco in each period.

4.2.1 The Pre-Indian Period

The fossil record indicates that the family Camelidae originated and developed in western North America, spread by way of the land bridges into Asia and South America in the Miocene, and finally became extinct in its original homeland (Simpson 1950). The fossil remains from the Pleistocene in Argentina indicate that there were formerly many more species of camels than the present four (Lopez 1930). Cabrera and Yepes (1940) report that the alpaca, llama, guanaco, and vicuna were already four distinct species in the Pleistocene. It is commonly believed that the alpaca and llama were domesticated by man from the wild guanaco and possibly the vicuna. However, the role that man played in the speciation of the domestic forms is still unclear, and the topic of current research.

Little can be said about the status of the guanaco in this period.

4.2.2 The Indian Period

The Indian period covers the time during which the Indians were the dominant ecological force in the Patagonian region. It begins with the first arrival of man, and ends with the displacement of the Indians by European colonists and their domestic stock.

While there is still considerable controversy over the time of appearance of aboriginal man in Patagonia and Tierra del Fuego, a reasonable estimate is 11,000 BP (Bird 1970). At this time giant ground sloths *Milodon* and other now extinct mammals were still roaming the pampas and forests of Patagonia. Coincidental with man's arrival a number of larger mammals became extinct: ground sloths, horses, mastodons, giant armadillos, large camel-like creatures, etc. Considerable controversy has developed about the cause of these extinctions, especially man's role. Martin (1970) hypothesized that early man, the hunter, built up locally to temporary high densities as the more vulnerable large mammals were being killed to extinction. Other hypotheses include dramatic climatic change resulting in loss of the habitats of these greatures (Webb 1978), competitive exclusion by more modern forms (Simpson 1969), volcanism, disease, and sea level changes (see Miller 1979, and Martin and Wright 1969). Which of these hypotheses is correct is not known. However, it is known that as man arrived, most of the large mammals of the region became extinct, leaving the guanaco to roam the temperate regions of South America free from competition with any other large herbivores. The only habitats of the temperate parts of the continent not occupied by the guanaco include the humid Valdivian forest and the extremely wet moorlands of Tierra del Fuego.

The guanacos of the Patagonia, including Tierra del Fuego, constituted an important part of the economy and culture of the Indians of the region. Gilmore (1950) writes that

> "In the extreme southern part of the temperate Neotropica, man built around the plains fauna, particularly the guanaco and rhea an ethnozoologic culture without domestication which is comparable to the bison-antelope culture of the plains indians and the caribou-elk (.ie moose) culture of the north

> woods and tundra indians, both of North America.... To the Tehuelche, Puelche, northeastern Araucanians, Haurpe, and Querand, the guanaco supplied meat for food, fur and hides for clothes and shelter, bezoar stones for medicine, sinew for sewing, pets for pleasure, a stimulus for myths and many verbalizations to account for age, sex, color, etc and an object of time consuming hunting activity for the men and the accessory duties for the women. Like the bison-hunting indians of Noth America, the guanaco-hunting Pampa Indiands were savage fighters, easily shifting their hunting techniques to warfare and fiercely resisting the inroads of the whites."

Barros (1963) stated that the Aruacanians of southern central Chile had domesticated the guanaco for use as a beast of burden, citing earlier authors who reported the Indians using guanacos as draft animals for plowing. However, the aboriginal Indians did not have plows, hence these reports have been discounted (Miller 1979). Except for the occasional pet, the Patagonian Indians did not have any substantial number of captive guanacos, and probably no domesticated herds. Rather they relied on hunting the guanaco with bolas, bow and arrows, and ocassionally dogs (Gilmore 1950).

While we have little direct information on the numbers of guanacos that existed during this period, we do have substantial circumstantial evidence that guanacos were extremely abundant in a wide range of habitats, and probably numbers in the tens of millions. At the close of this period, Darwin (1845:142) stated that: "the guanaco....an elegant animal...is the characteristic quadruped of the plains of Patagonia.... It is very common over the whole of the temperate parts of the continent." He went on to state that on the shores of the Rio Santa Cruz in the southern Patagonia of Argentina, he saw herds of up to 500 guanacos.

Prichard (1905:27) wrote that "literally thousands appeared on the summits of the surrounding ridges." Musters (1871) recorded seeing herds some three to four thousand strong. Rogers (1877) estimated that there were 1,500,000 guanacos in the region south of the Santa Cruz river in Argentina. His estimate was an extrapolation from the Indian population size and hunting patterns.

It is not unreasonable to estimate the aboriginal guanaco population to be in the order of 30 to 50 million. The aboriginal guanaco range is now cultivated to a large extent, and still supports over 45,000,000 sheep and 25,000,000 cattle. As late as the 1920's, Romero (1927) estimated the remaining guanaco population to be 3,000,000, and this was after the region was well settled and the cattle and sheep industry was at full production.

Neither predation or Indian hunting pressures seems to have been sufficient to limit the number of guanacos, except around the areas of traditional habitation. The guanaco population was presumably at the carrying capacity of the habitat, and thus limited by food resources during the critical part of the year. This hypothesis is supported by the observations of Darwin (1845) and Stassen (1916) who reported on the existance of large "guanaco cemeteries" where guanacos reportedly went to die. This idea still persists, even though Prichard (1902) explained that these bones were the remains of guanacos that had perished in severe winters, after congregating in the areas of reduced snow accumulation, or where some brush remained for foraging.

Figure 15, adapted from Dennler de la Tour (1954) shows the distribution of the guanaco in the 18th century, before the arrival of European man, and the reduced distribution of the 1950's.

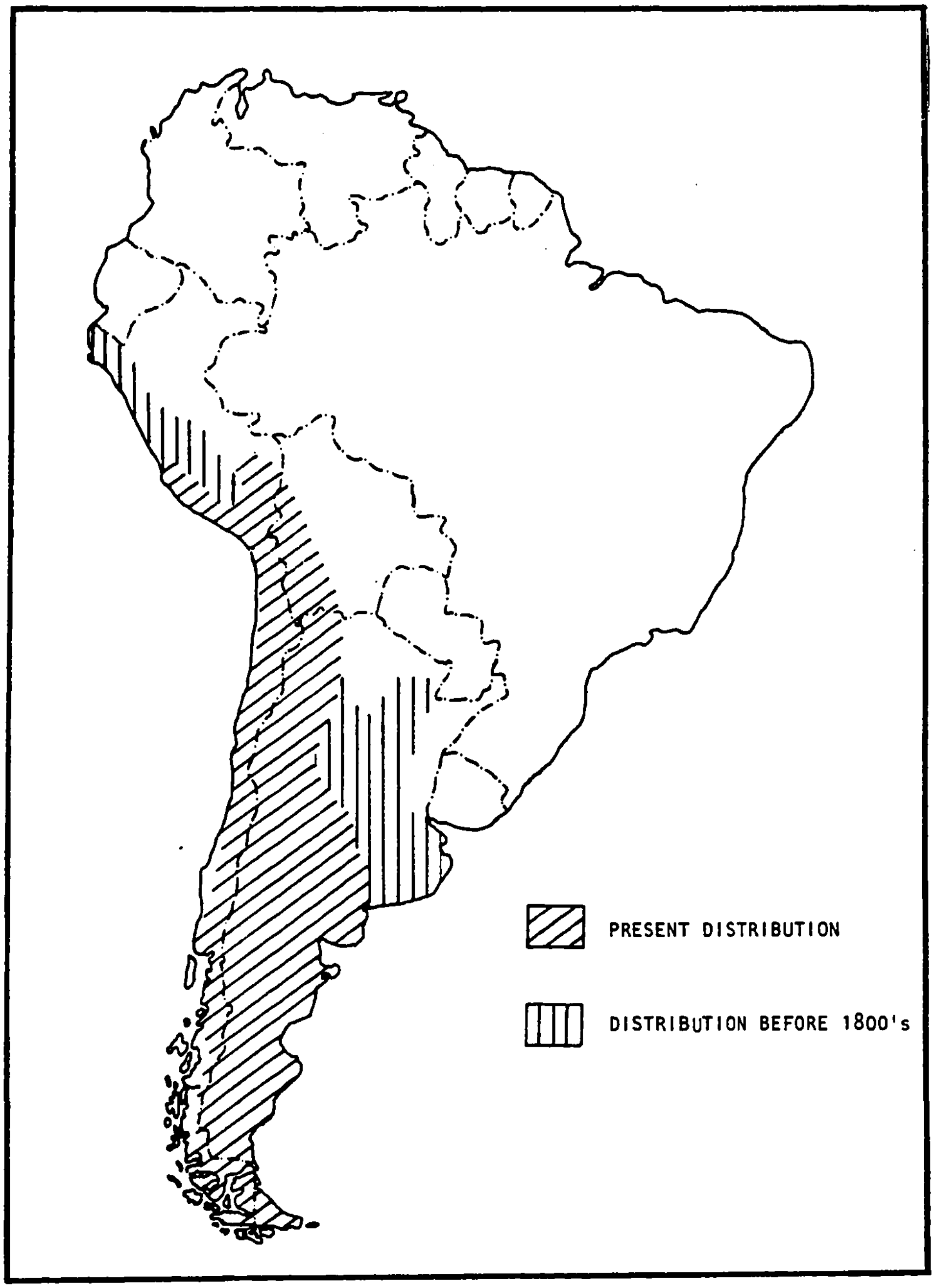

Figure 15. The aboriginal and present distribution of the guanaco in South America, adapted from Dennler de la Tour (1954).

4.2.3 European Colonization (1850's to 1950's)

During coloization period the guanaco fared badly. Their range was preempted in large part by the livestock and farming industries, while their populations suffered from uncontrolled hunting for hides and meat. The guanaco was reduced from the characteristic quadruped of the pampa to a threatened and declining species.

In Magallanes and South America in general, the principal decline of the guanaco was related to the rapid development of the sheep industry. In the province of Magallanes, the domestic sheep population rose from 800 in 1877 to 2,625,000 in 1931 and stabilized at about 2,900,000 in the late 1960's (Erasmo 1972). With the sheep came many changes. Bridges (1948) indicated that the pampas changed from a tall-grass to a short-grass community. This was accompanied by an increase in the wild goose (caiquen) population that thrived on the short-grass community and are are now considered a plague in the region. After 1935 the sheep populations stabilized and actually began to decline in some areas, presumably as a consequence of overgrazing.

In an earlier paper (Raedeke 1978), I hypothesized that competition with domestic sheep was the principal cause of the guanaco decline in this period. This hypothesis is the subject of the present study, and will be discussed in detail in the following sections.

Guanaco numbers were apparently reduced not only through competition with sheep that occupied their former range, but also by the accompanying personnel and management practices. The poorly paid sheepherders were encouraged to augment their low wages by hunting guanacos. Furthermore, fences that were constructed for sheep pasturing entangled and killed thousands of guanacos. One large estancia on Isla Grande had a crew of men that did nothing by but clear the fences of guanaco carcasses for the first few years after construction in the early 1900's (D. McDonald per. comm.). Forests and other marginal sheep ranges, used by guanacos for winter cover, were cleared by burning to increase sheep production. At one time there was a bounty on guanacos as they were considered pests (Bridges 1948). It was even suggested that a disease be introduced to eliminate the guanaco (Romero 1927).

Commercial hunting also played an important role in the reduction of guanaco numbers. Stassen (1916) reports that from Argentine province of Chubut between 30 and 40 thousand chulengo hides were exported to Germany in one year alone. On Isla Grande, numerous individuals made their living by hunting chulengos. An older sheepherder, who has spent his entire life on the island, reported that in about 1940 over 1,000 chulengo hides were harvested in the central part of the island alone. Allen (1942) reported that in 1928, 300,000 guanaco hides (of all age classes) were exported from Argentina.

Many sheepherders felt that the extreme hunting pressure in the 1930's and 1940's on the new-born chulengos had reduced recruitment to zero and that the entire population was about to crash (Dennler de la Tout 1954). Adults were less prized since their wool was short, and the meat was considered to be good only for dog food.

In the 1930's most of the South American countries with guanaco populations enacted laws that gave the guanaco limited protection. The kill was generally limited by law to the adult males, and the chulengos were fair game only during a restricted season of the year. However, most of these laws were either unenforcable or ignored. In fact, the well armed national police and military, charged with the enforcement of the laws, were often the most flagrant violators. Accounts of police shooting guanacos and vicuna with machine guns are common in the literature (Dennler de la Tour 1954 and Jungius 1971).

The decline in the guanaco population is best documented in Argentina, which had by far the largest aboriginal population. Romero (1927) estimated that by the 1920's the population had declined to 3 million. Cardozo (1954) estimated the same population to have been further reduced to 300,000 by 1948. There is little information on the decline in Chile, but it presumably followed that same pattern. Figure 15 shows the reduction in the aboriginal range distribution of the guanaco by the 1950's.

4.2.4 Present Guanaco Populations

In recent times the status of the guanaco in South America has continued to deteriorate. The population numbers have declined and the distribution has been reduced. Less than one percent of the aboriginal population survives, and especially in the northern part

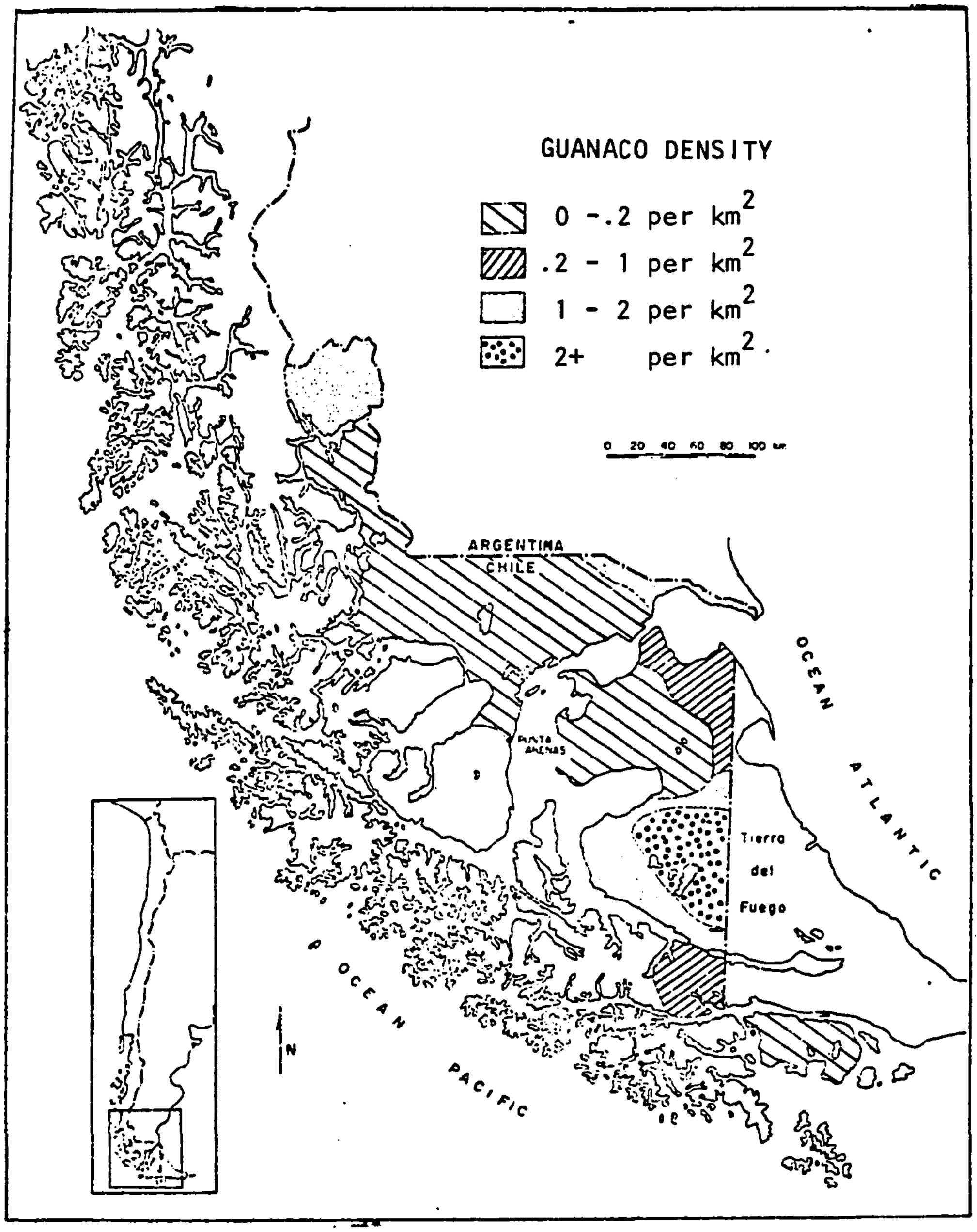

Figure 16. Distribution and abundance of the guanaco in Magallanes, Chile, 1975.

of the range, remnant herds are small. The guanaco must now be considered at least to be "vulnerable" and probably "threatened" over much of its range (IUCN classification system, see Miller *et al.* 1973).

The principal causes of the continued decline are not unique to the guanaco, but rather are common phenomena in developing countries. First, other tha legal protection, with only sporadic enforcement, there is no active management of the species in any part of South America. This is mainly due to a lack of knowledge about the species life history necessary for the development of a management program. Second, while sheep numbers have stabilized, the herds are held above the carrying capacity of the range, so the range continues to deteriorate (Howard 1969), despite efforts in range management (Erasmo 1972). These problems and their effects on the guanaco population will be discussed in detail in the later sections.

4.2.5 Current Guanaco Population Size

The total population of guanacos in South America in 1973 numbered approximately 125,000, distributed as follows: Argentina - 109,000 (Nuevo 1975), Chile - 13,000 (Miller *et al.* 1973), Peru - less than 5,000 (Grimwood 1968), Bolivia - no verified population (Bejerano, per. comm.). The decline of the guanaco population is best documented for Argentina, and is given in Table 3.

Table 3. The decline in the guanaco population of Argentina since 1926.

Year	Population	Source
1926	3,000,000	Romero (1927)
1954	350,000	Guildbride (Cited by Nuevo 1974)
1970	300,000	De Caro & Nuevo (1973)
1973	281,000	Nuevo (1974)
1974	109,000	Nuevo (1974)
1975	70,000	Raedeke (1978)

4.2.6 Present Guanaco Distribution

The current distribution of the major guanaco populations in Patagonia is known only in broad outline. For the most part, the guanaco has been eliminated from the large and fertile pampas as a result of competition with sheep, illegal hunting, and deterioration of the range due to overgrazing. The guanacos are now found in the less accessible, rough or scrub lands (Howard 1969). Small numbers are found throughout the range as described by Dennler de la Tour (1955) (see Figure 15). However, the present distribution must not be considered to be continuous, but rather to consist of small isolated populations of varying status, and only local abundance.

In Magallanes, extensive surveys were conducted from 1972 to 1975 to document the distribution of the guanaco more precisely. Figure 16 shows the distribution and relative densities of the guanaco in 1975 throughout the province. The total population was estimated to be 10,000 individuals, with 7,000 on Isla Grande, and the remainder on the mainland. These estimates are based on six aerial surveys, and eight road transect censuses (Raedeke 1978). Throughout Magallanes, the guanaco is limited to the national parks, rugged marginal sheep range, forested areas, and to several of the large estancias that still

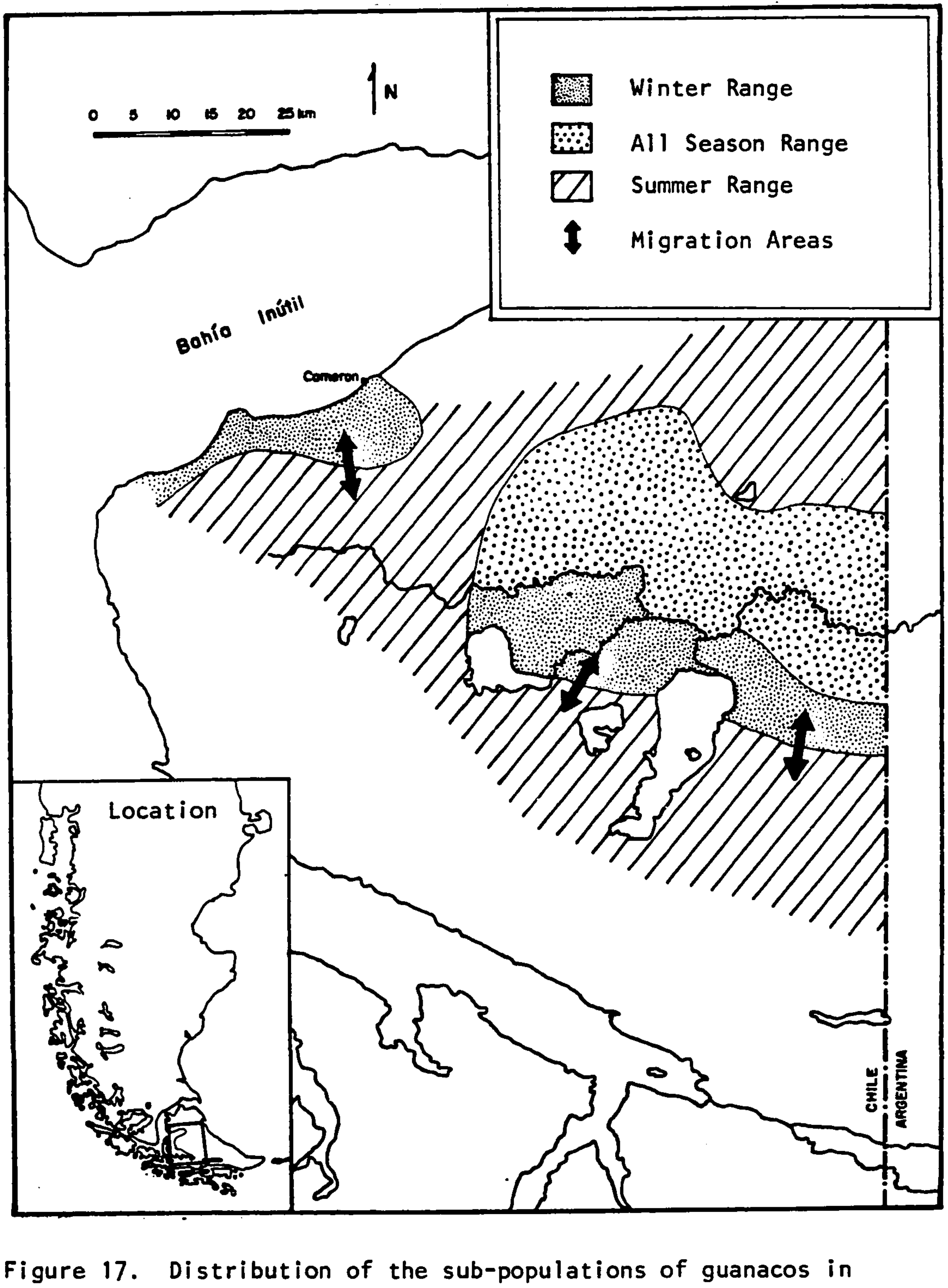

Figure 17. Distribution of the sub-populations of guanacos in southern Isla Grande, Chile.

exist, where sheep ranching is not as intensive as on the smaller, privately owned ranches.

The guanaco study area, roughly corresponding to the Estancia Cameron of 2,000 square kilometers had (in 1973) an estimated guanaco population of 5,000, or 50% of the total population of the province. This large estancia, located at the southern extreme of the profitable sheep range, contained this large guanaco population because there was adequate winter cover and browse, the area was marginal as sheep range, management was not intensive, and there was little guanaco hunting. The dynamics of the Estancia Cameron guanaco population will be discssed in detail in a later section.

Within the study area, and all along the foothills of the Andes, one finds both seasonally migratory and non-migratory guanacos. The seasonally migratory guanacos move up in elevation in the spring, following the retreat of the snow. In map distance, the maximum movements are about 40-50 kilometers between winter and summer range, with an elevation gain of 600 to 1500 meters. The migrating guanacos pass from the southern Rio Grande basin grasslands through the deciduous forest, and spend most of the summer on the meadows in the precordillera. While the majority of the guanacos in the area inhabited by the migratory population do migrate seasonally, one can still find guanacos in reduced numbers on the winter range area in all seasons of the year. The non-migratory guanacos are found principally to the north of the Rio Grande. In this region the guanacos do not make any predictable seasonal movements. However, they are somewhat nomadic due to disturbances caused by domestic stoc movements. These two populations are quite distinct, however, they are not geographically isolated. The distribution of these two sub-populations is given in Figure 17.

The biology and life histories of these two populations differ greatly, and they will be compared, and analyzed separately whenever possible.

CHAPTER 5

Growth and Condition

The guanaco has been characterized as an elegant animal (Darwin 1845), as "ill-proportioned and awkward" (Allen 1905:20), and as "the least handsome and most stupid" of all the animals of Patagonia (Simpson 1934:190).

In appearance, the guanaco looks like a small humpless camel, with the long legs of a colt, a long slender neck, a short and bushy tail, and feet with broad flat pads behind divergent hoofs. The head is camel-like, horns are never present, the ears are long and pointed, and the lips are highly mobile and deeply cleft. The guanaco is distinguished from the similar looking vicuna by the presence of callosities on the inner side of the

Figure 18. An artist's portrayal of the guanaco in its natural habitat on Isla Grande.

forelimbs, and the lack of the characterisitc white or yellowish bib of the vicuna (Walker 1963). The general color of the guanaco is a reddish brown, with a grayish colored head, and white underparts. Figure 18 gives an artist's portrayal of the guanaco in its natural setting on Isla Grande.

To the casual observer, both sexes look alike. They are identical in coloration, and similar in size. In the field, behavioral differences provide the only quick means of sexing individuals. However, careful measurements reveal differences in conformation between the sexs, as will be detailed in a later section.

The guanaco is the largest of the wild ungulates of temperate South America. However, it is smaller than the domestic llama, which has been bred as a beast of burden. Table 4 gives the average measurements for all adults guanacos collected in this study. When we compare these measurements with those of other authors, given in Table 5 we find that the guanaco of Isla Grande is the heaviest of the reported guanacos. Osgood (1916), Allen (1942), and Lonnberg (1913) made the generalization that the southern guanacos were the largest of the species, based on various measurements, including the skull. However, when we compare the other body measurements, the trend is not so

Table 4. Average adult body measurements for guanacos from Isla Grande, Chile.

	All Adults			Adult females			Adult Males		
	Sample size	Average	S.d.	Sample size	Average	S.d.	Sample size	Average	S.d.
Total Length[1]	19	190.8	7.2	11	191.5	7.8	8	189.8	6.4
Total Weight[2]	19	120.2	12.2	11	121.3	14.3	8	118.7	9.1
Carcass Weight[3]	16	68.5	7.9	10	69.1	8.7	6	67.6	6.8
Chest Girth	23	110.3	8.4	13	113.9	2.8	10	105.7	15.7
Ear Length	20	13.3	0.6	11	13.4	0.6	9	13.2	0.8
Shoulder Height	18	115.3	5.5	10	113.8	5.4	8	117.2	5.8
Hind-foot length	41	50.2	1.5	17	49.4	1.5	24	50.8	1.5

1. Total length is from the tip of the nose to the base of the tail.
2. For females the reproductive tract weight has been subtracted from the total weight.
3. The carcass weight is the total weight after removal of the visera, hide, skull, and feet

All length measurements are in centimeters, and weight measurements in kilograms.

Table 5. A comparison of the body measurements of guanacos from different regions.

Body Part	Romero	Allen	Caberra & Yepes	Walker	Stassen	Osgood	Cardozo
Total Length	199	195-215	185	120-175	200	130	215
Chest Girth	112	127	-	-	-	108	-
Shoulder Ht.	111	-	110	90-100	150	-	111
Tail length	25	-	27	25	24	-	25-27
Total Weight	105	-	-	48-96	60-75	-	48

Sources and Locations: Romero (1927), Peninsula Valdez, Chubut, Argentina; Allen (1905), Cape Fairweather; Caberra & Yepes (1940), unknown locations in Argentina; Walker (1963), unknown locations, probably from literature; Stassen (1916), unknown locations; Osgood (1916) near Puno, Peru; Cardozo (1954) unknown locations, probably Boliva near Lake Titicaca.

clear. In fact, the guanaco of Tierra del Fuego is only larger in skeletal size than the guanacos measured by Walker (1975), Cabrera and Yepes (1940) and Osgood (1916), which were collected at different extremes of the geographic range of the species, and not as large as those of Romero (1927), Allen (1905), Stassen (1916) and Cardozo (1954). The inconsistencies in these recorded measurements might be due to the inclusion of the sub-adults in the sample, and imprecise measurement, especially in total weight. Until more data is available, we can say little about the ralative body size over the range of the species.

5.1 Growth

A knowledge of the growth patterns of a species is useful in calculating the biomass and yield of a population, and in the comparison of the well being of different populations.

5.1.1 Post-natal Body Growth

The size and growth of an organism is correlated with sex, age, nutritional levels, and genetics (Nellis 1962, Wood and Cowan 1968). Nutrition and genetics are considered to be the ultimate factors influencing the adult body size in ungulates, while age is the primary factor in early life (Nellis 1962, Anderson *et al*. 1964,, Bandy *et al*. 1956, Park and Day 1942, Johnson 1937, and Taber 1956b). Models of growth should then be based on sex, age, nutrition, and genetics to be most meaningful.

A large number of suitable mathematical models have been developed to describe post-natal growth (see Huxley 1932 and Brozek 1963). While many elegant procedures are currently in use, the suitability of any mathematical model must obviously depend on the extent to which it describes the actual process in a biological sense. Wood and Cowan (1968:111)) suggest that until more data become available, "little purpose is served by the application of elaborate mathematical procedures to the growth curves of wild herbivores...it would seem that a simple course of growth curve provided the most meaningful expression of events."

Sufficient data have been collected on the guanaco in the present study to model post-natal growth of the following parameters: total weight, total length, hind-foot length, and the length of the mandible. The von Bertalanfy (1938) growth curve has been used to model the guanaco growth, and it has the follwing form for the length parameters:

$$L=Lm(1.0-exp(-age+to)(k))) \qquad (1)$$

where "l" is the length, "Lm" is the asympote of the curve, or the maximum length attained, "to" is the age when length is zero, and "k" is the growth rate parameter. The formula for growth in weight is the following:

$$W=Wm(1.0-exp(-(age-to)(k)))***3 \qquad (2)$$

where "W" is the weight, and "Wm" is the asymptotic weight attained, and the other parameters are identical to equation (1).

The growth data has been analyzed by nonlinear regression, using the BMBX85 routine (Dixon 1970), and was compared to results from the SPSS nonlinear regression routine (Nie *et al.* 1970). Table 6 gives the estimated regression equation parameters, and the results of the tests for sexual dimorphism. Figures 19, 20, 21, 22, 23, and 24 plot the growth curves and the data points.

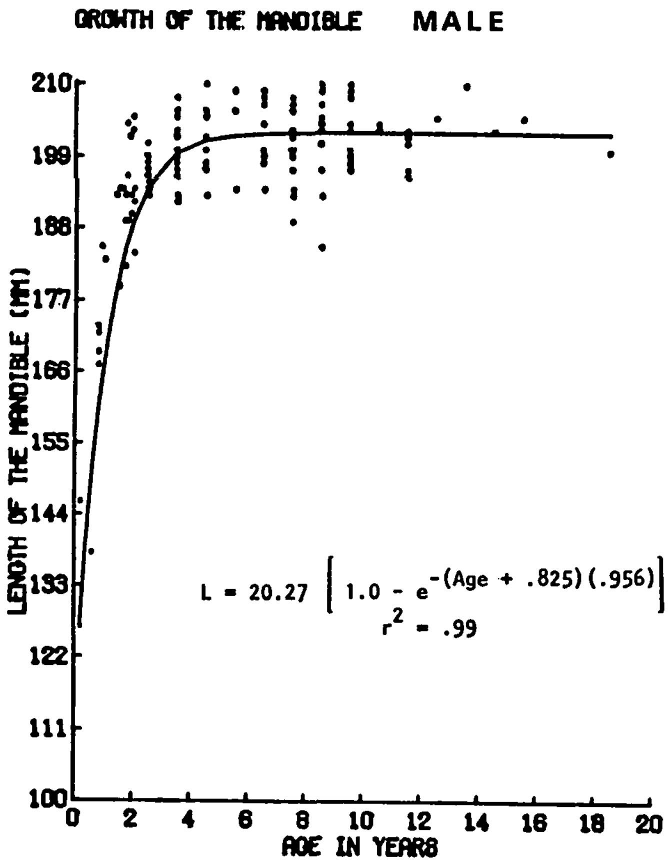

Figure 19. Growth of the mandible in male guanacos.

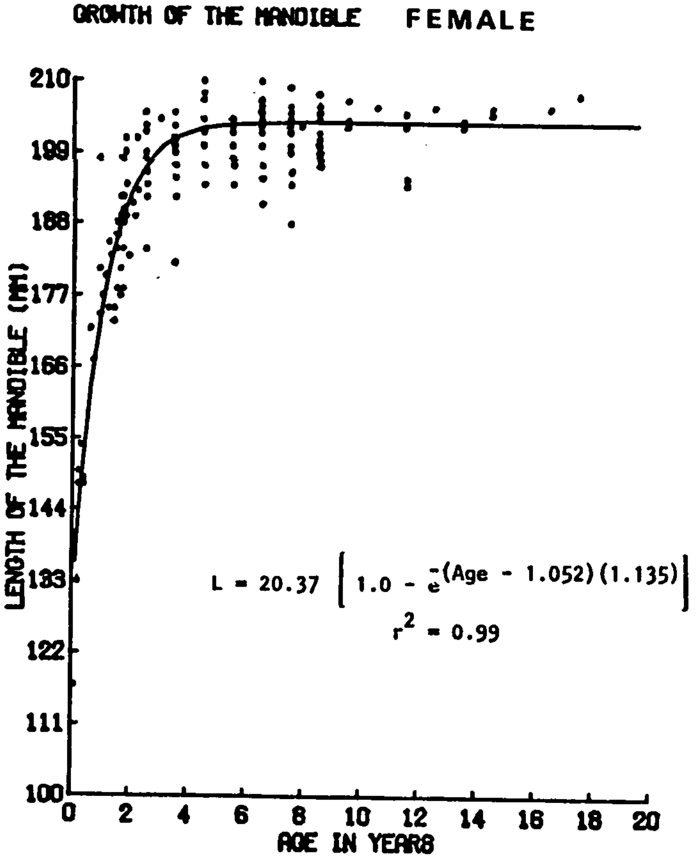

Figure 20. Growth of the mandible in female guanacos.

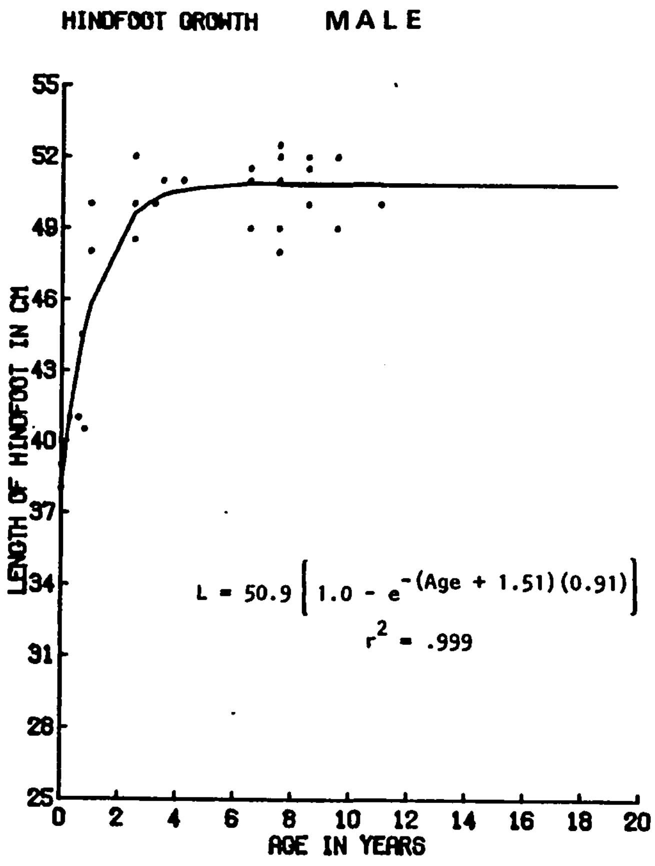

Figure 21. Growth of the hindfoot in males guanacos.

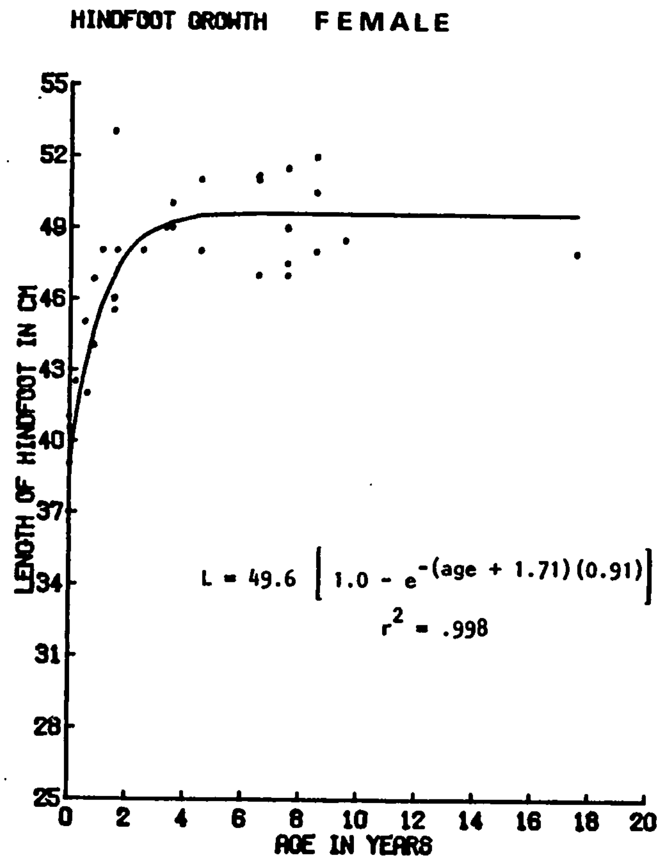

Figure 22. Growth of the hindfoot in female guanacos.

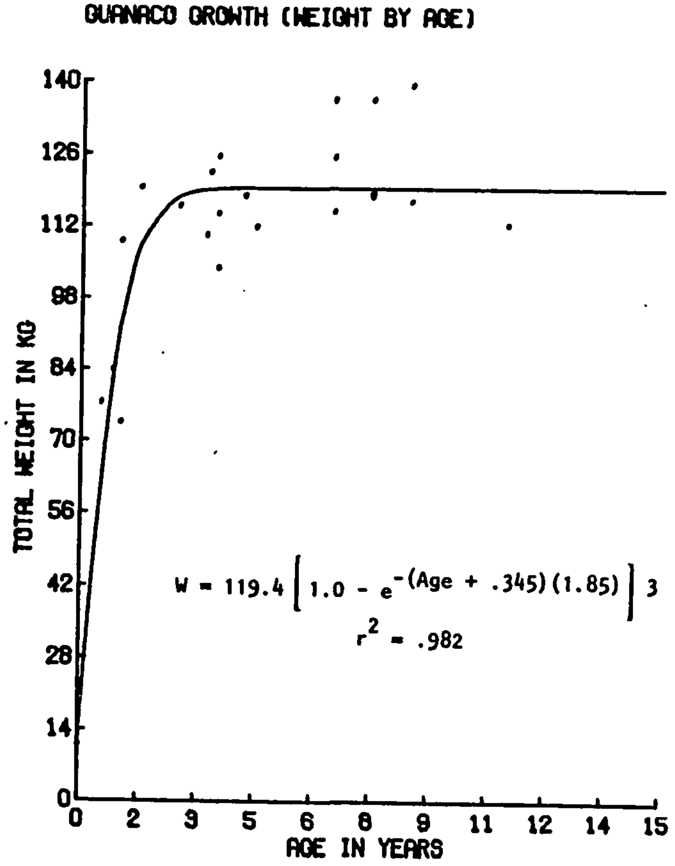

Figure 23. Growth in total weight in male and female guanacos.

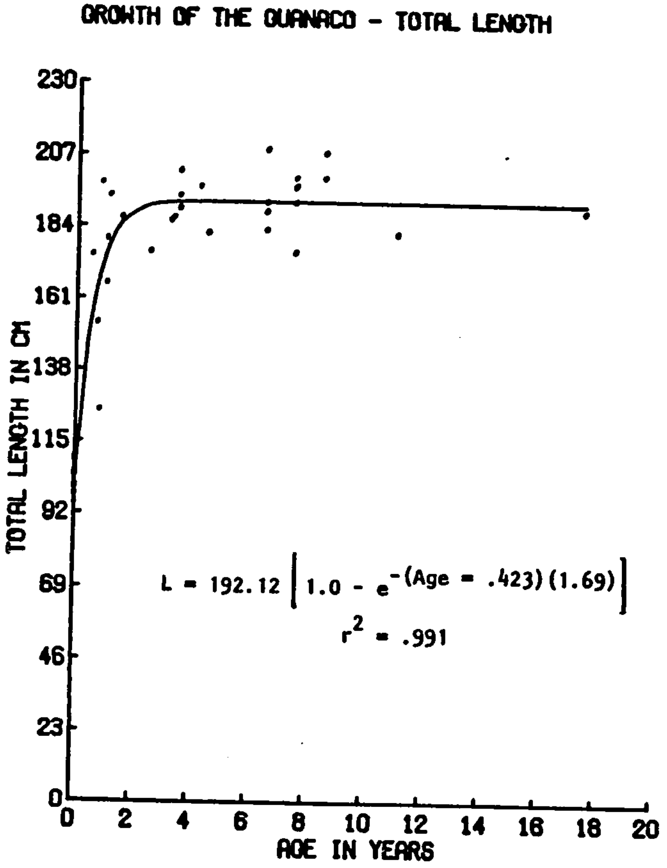

Figure 24. Growth in total length in male and female guanacos.

Table 6. Estimated regression parameters for the guanaco growth models. The differences between the sexes are compared for all values.

Parameter	Sex	L_m or W_m	k	t_o	Sample Size
Hind-foot length	M	50.91	.912	-1.512	34
	F	49.64	.905	-1.717	41
P values		<.005	>.05	<.02	
Mandibular length	M	20.27	.956	-0.825	148
	F	20.37	1.135	-1.052	166
P values		<.001	<<.001	<<.001	
Total Length	M	191.41	1.013	-0.774	17
	F	193.96	3.708	-0.201	20
P values		<.02	<.005	<<.001	
Total Weight	M	118.44	1.858	-0.329	11
	F	120.08	1.824	-0.544	14
P values		>.05	>.05	>.05	

All length measurements are in centimeters, and weights are in kilograms. The total weight of the females has been corrected by subtraction of the weight of the reproductive tract.

The growth pattern of the guanaco follows that of many ungulates, with most skeletal growth occuring the first two years of life (Nellis 1962). An individual reaches 80 to 85% of adult size by two years of age, and by three years of age the individual guanaco has reached full adult body size. The epiphyses of the long bones begin to fuse at age three years, and by age four, no further growth in length is possible. However, weight continues to increase even after skeletal growth has stopped. This is the general pattern for all growth parameters measured in this study.

This pattern of growth makes it difficult to make field classifications by individual ages beyond the age of three years. Past three years, size is not highly correlated with age. Furthermore, while the 0 to 1 age class is quite distinct from the older age classes, the 1 to 2 year-olds are not readily distinguishable from the 2 to 3 year-olds. Any attempt to classify animals that are almost two years of age (i.e. yearlings in December) will result in considerable error.

The general hypothesis of this study, that the guanacos are in direct competition with the sheep, and have been displaced from the prime range, can be tested indirectly through an analysis of growth. Since growth is a function of nutrition (Brody 1945, Maynard and Loosli 1956, Bandy et al. 1956, Anderson et al. 1964), we would expect that animals occupying marginal range would tend to be smaller in size, and grow more slowly. Hence, I would hypothesize that the seasonally migratory guanacos that occupy range areas that are on the fringe of the historic guanaco range, would be at a lower nurtitional plane, and hence be smaller and grow more slowly than individuals which still occupied excellent habitat.

To test this hypothesis, the growth functions of the two sub-populations are compared for each sex. The parameter to be analysized is the length of the the lower jaw, since this is the only parameter for which sufficient data exists for both groups. The results of the tests are given in Table 7. We find that the resident guanacos, those occupying the traditional range areas of the guanaco, are larger (they have a larger Lm), and they grow faster (they have a larger k) than the migratory guanacos. The smaller "to" (the age when length is zero) also reflects a more rapid growth. As we can see from the table, the pattern is identical for both sexes, and the diffrence are highly significant in most cases.

From this test, we can conclude that the migratory guanacos are truly smaller than the resident guanacos, and that this is probably due to their lower level of nutrition. An alternative hypothesis of genetically isolated sub-population is not tenable, since these two

Table 7. A comparison of growth parameters in migratory and non-migratory guanacos of Isla Grande, Chile.

MALES

Sub-populations	L_m	k	t_0	Sample Size
Migratory	203.56	0.7957	-1.421	106
Non-migratory	203.94	1.2951	-0.658	60
P values	<.05	<<.001	<<<.001	

FEMALES

Sub-populations	L_m	k	t_0	Sample Size
Migratory	202.46	0.3735	-6.254	78
Non-migratory	204.60	1.1480	-0.808	70
P values	<.005	<<.001	<.005	

groups of guanacos are not geographically isolated. Indeed, the social organization of the species, with territorial males, and a high degree of polygyny, and forced emigration, would surely guarantee a high degree of gene flow between these groups. This hypothesis will be examined again through an analysis of demographic vigor in a later section on population dynamics.

5.1.2 Growth of the Eye Lens

The weight of the eye lens has been used to determine the age in a variety of animals (Taber 1963). The technique was based on the work by Lord (1959) who found that the eye lens of mammals grows continually throughout life, and that the weight of the lens could be correlated with the age of the animal. Later studies have shown that the weight of the lens can also be used as an indicator of nutritional level of the population, and the well being of the different populations could be compared by an analysis of the eye lens growth functions (Lord 1962).

During the present study, eye lens weights were obtained from 24 guanacos aged by tooth cementum annuli and tooth replacement (see Appendix A). The weights of the lenses were related to age through regression of the following equation:

$$W = a + bX**k \qquad (3)$$

where "W" is the weight of the lens, "a" is the weight of the lens at birth, "b" and "k" are the growth parameters, and "X" is the age of the guanaco measured in years. The growth of the lens, based on this regression is shown in Figure 25. The sexes have not been treated separately, due to small sample size, even though a difference in lens

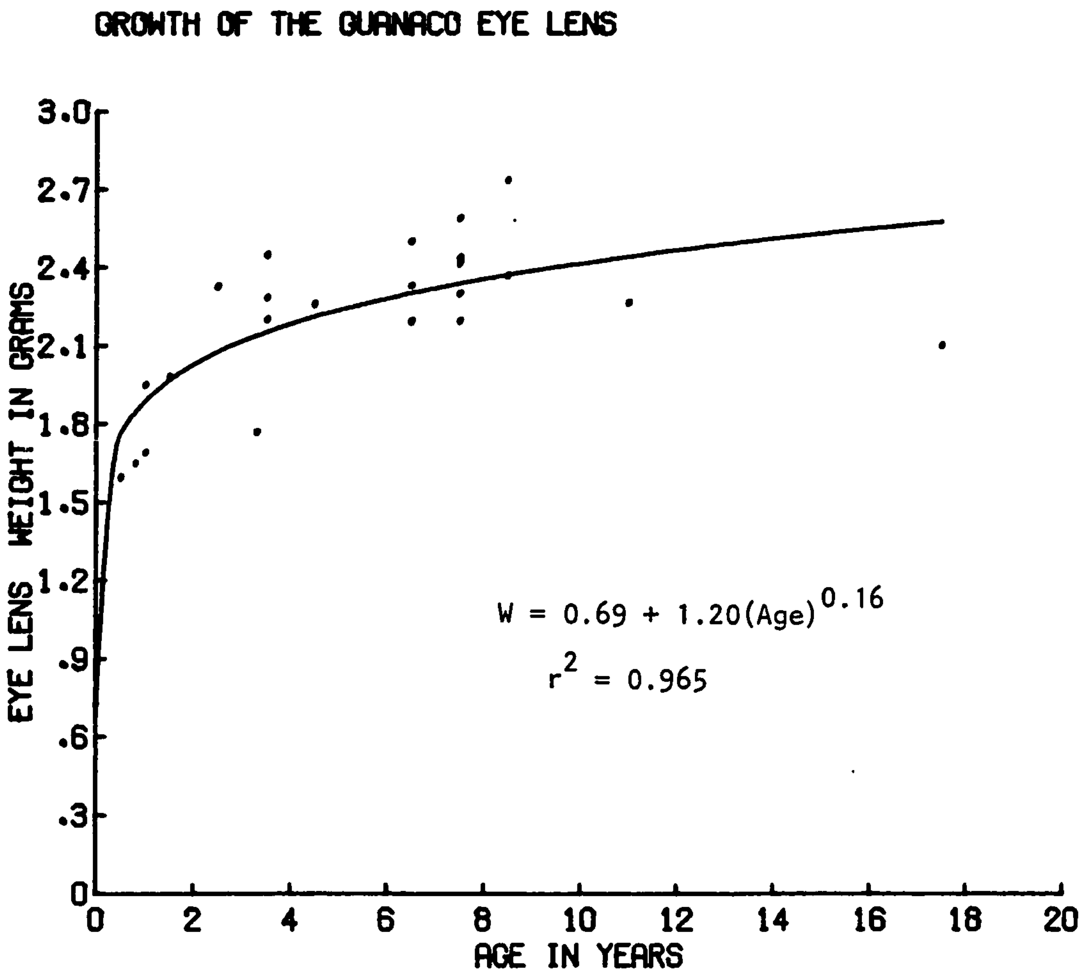

Figure 25. Growth of the eye lens in guanacos from Isla Grande. Both sexes are included in the sample.

weight between sexes has been demonstrated for the Columbian black-tailed deer by Longhurst (1964).

From the Figure 25 it is obvious that the lens weight can be used to distinguish only between the chulengos (less than 1 year of age), yearlings, and adults. However, these age classes are much more readily identified by examination of the dentition or other body parameters. Therefore, the greatest promise for the lens growth analysis would seem to be for the comparison of nutrition levels between the different guanaco populations when more data becomes available.

5.2 Sexual Dimorphism

Charles Darwin (1871) puzzled over the question of why males and females of the same species often are so greatly different from each other in appearance, size and behavior. He concluded that sexual selection, a form of natural selection, "shapes the anatomical, physiological, and behavioral mechanisms that function shortly before or at the time of mating, and serve in the process of obtaining mates...Darwin reasoned that competition for mates among members of one sex leads to the evolution of traits peculiar to that sex" (Wilson 1975:318). The process of sexual selection is now referred to as "intersexual" and "epigamic" selection (Huxley 1938).

The results of sexual selection are the dimorphic features that increase the individual's competitive abilities to obtain a mate, such as large size, rapid growth, and organs of threat and combat such as antlers, tusks, manes, and canine teeth (Barash 1977).

Since guanaco males actively fight for, and defend territories as a means of obtaining access to reproductive females, and females do not compete for males, we would expect that males would have evolved sexually selected characteristics, such as those listed above.

To test for sexual dimorphism, the growth functions were compared between the sexes. Secondly, the size and growth of the canine teeth of the two sexes were compared.

It has long been known that the sex in the lamoids can be determined by examination of the canine teeth (Lonngerg 1913, Cabrera and Yepes 1940, Bridges 1948, Koford 1957, and others). Koford (p. 199) states that for the vicuna "the female (canine) teeth extend six millimeters from the base of the jaw, and 12 millimeters in male". However, in guanacos, the canine length alone is not a distinguishing characteristic, since there is considerable overlap between the sexes. But when the overall mass of the tooth is considered, there is no overlap. Raedeke (1978) developed a "canine index" by multipying the height of the canine by the maximum diameter at the alveolar rim. This index, combined with a knowledge of the age of the individual allows complete separation of the sexes. Figure 26 shows the correlation of the canine index with sex and age for 120 males and 141 females. The solid line connects the average for each age class, and the vertical lines represent the absolute range. No data are plotted for the 0 to 1 age class, since the canine tooth erupts from the gum only at the age of 1 to 2 years (see Appendix A). These data clearly demonstrate that the guanaco has sexually dimorphic canine teeth.

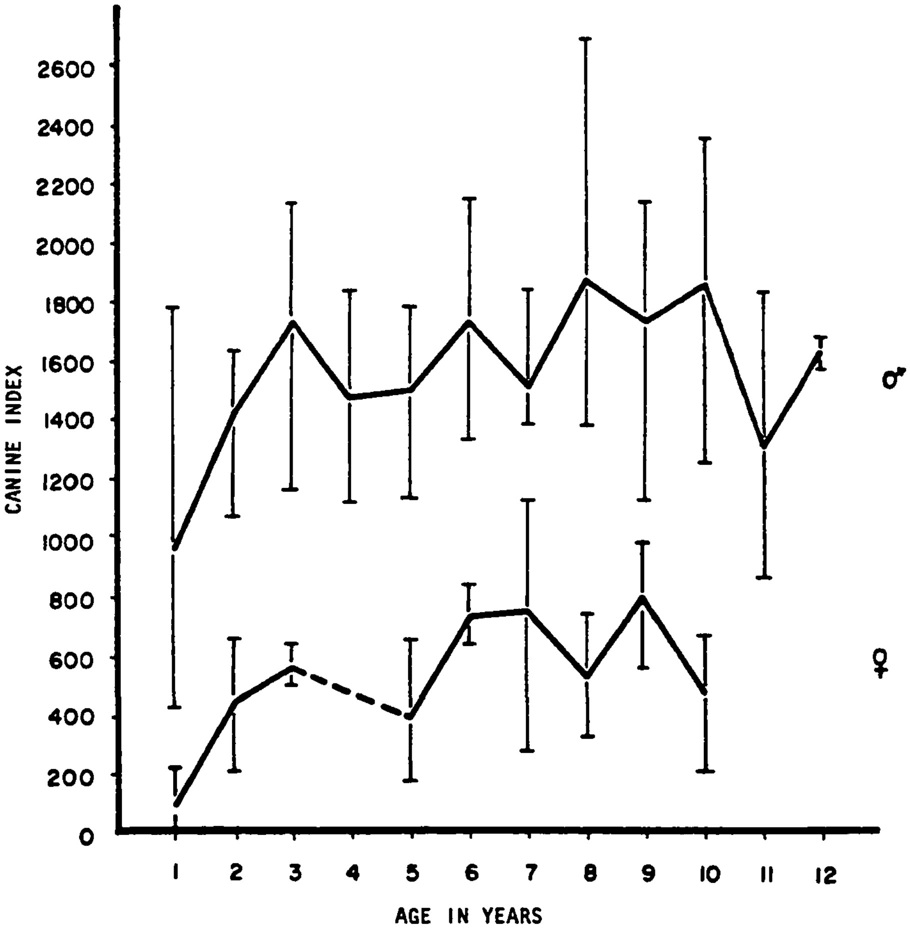

Figure 26. A comparison of the "canine index" with age. The horizontal bar connects the means, and the vertical bars give the absolute range in each age.

Active physical combat between males for territories and thus access to females should select for males that would be more successful in these fights. Alexander *et al.* (1978) hypothesized that the degree of sexual dimorphism should be a function of the magnitude of polygny, and have developed a regression model that correlates body size with polygny for a large number of mammalian species. However, the guanaco and the vicuna are not as dimorpic as is "predicted" on the basis of the regression analysis.

Several hypotheses have been proposed to explain the lack of obvious sexual dimorphism in camellids. Franklin (1978:157), working with vicuna, suggested that since females are permanently with the males on year round territory, "they can base their selection (of a male) much more on the acutal resources of the site (than on the physical characteristics of the male). In addition, the males access to estrus females has already been determined long before the breeding season, so males do not directly compete for females". The obvious problem with this hypothesis is that the males with territories, hence selected by the females, are the best able to compete for territory. Therefore we would again expect males to be sexually dimorphic. Furthermore, as we will see in a later section, territorial guanaco males are most frequently tested immediately before the breeding season. Territorial males that are unable to defend their territory are displaced, and the winner then has access to the estrus females. Koford (1957) also observed this to be the case in vicuna.

Paul Sherman (per. comm.) suggested that for the vicuna, the big males may have been consistantly shot by the local poachers, thus selecting for smaller males. While this may be the case in vicuna, who have been in contact with humans for many centuries, there has been no such selection for large male guanacos by the Patagonians. In fact, there has been a selection against the males, since their hides are of lower quality, and their meat less palatable. Further, the guanacos of Patagonia have been in contact with humans for a much shorter period of time than have the vicuna.

Until the present study, the lack of detailed growth data has precluded the testing of the initial hypothesis of sexual dimorphism in size in guanacos. Estimates of body size have been made by eye, there being few actual measurements of body size. Having sufficient skeletal measurements to test the hypothesis that sexual dimophism actually exists, I modeled the growth of the total weight, total length, hind-foot length, and the mandibular length, and then compared the the resulting regression values using a Rao Chi-square test of the asymptotic deviations of the parameters (Rao 1973). The results of the analysis are given in Table 6 in the section on general growth. The differences are considered to be significant if the P value is less tha 0.05.

This analysis shows that males are smaller than females in some measurements, and larger in others - i.e. their body conformation is different. The males weigh less than the females, are shorter in head and body, but larger in hind-foot length - that is, they have more compact but taller bodies.

From these results I would conclude that the guanaco is truly sexually dimorphic, and speculate that selection for height and canine tooth size in males is due to their method of fighting, and territorial defense. Since the guanaco is historically an animal of the open plain, speed would be highly adaptive in territorial defense and combat. In addition, guanacos do not traditionally engage in combat that would select for large body size, such as the ramming of sheep (Geist 1971) or the head long charges of bison (Fuller 1960) and elk (McCullough 1966). Rather, they chase, bite, and wrestle with their necks. This type of combat could be selective for the taller, more compact body, speed (longer legs), and larger canine teeth of the male guanaco.

The tremendous physiological cost of continual yearlong terriorial defense could select for smaller body size in the males. A smaller body, with the consequent lower total nutrient requirement, could be a selective advantage. For example, Belovsky (1978) calculated that in the absence of sexual selection, the optimum size of the bull moose should be smaller than that of the female, based on energetic and foraging constraints (200 kg. for males versus 307 kg. for females). A smaller male, with lower nutritional requirements might be better adapted to withstand the rigors of territorial defense. Koford (1957) and Franklin (1978) both remark on the high cost of territorial defense in vicuna, and the reduction in time available for foraging. Male guanacos face the same physiological drain, and as a result are generally in poorer condition than the non-territorial males (see the following section for details on condition). Struhsaker (1967) found that adult harem bull wapiti spent less than one-half as much time feeding as did cows, and more time in energetically expensive activities related to the maintaining their harem. Flook (1970) documented the subsequent decline in condition of these harem bulls during the short period (30 days or less) when the wapiti bull is in rut. He further documented the partial recovery of condition after the cessation of the rut, before the onset of winter. Even with a partial recovery of condition, the harem bulls are less likely to survive the following winter (Flook 1970, McCullough 1966). Since the guanacos continue to defend their territory after the rut, there is no period when condition can be readily regained. Hence, the large body size of the bull wapiti, with its high cost of maintenance, could be a disadvantage for yearlong territorial defense.

Interestingly, the species that are less dimorphic in body size then "predicted" by the model of Alexander *et al.* (1978) are territorial yearlong: the two camellids and two species of territorial zebras. Thus the ability to successfully compete in physical combat may be a trade-off with the ability to defend the territory the yearlong.

5.3 Condition

The physiological condition of ungulates of temperate regions tends to follow a cyclic pattern in response to the quality and availability of their resources (Brody 1945, Riney 1955, Bandy *et al.* 1956, and Taber and Dasmann 1958). Condition is defined as "the level of energy reserves of the animal with respect to internal and external demands" (Taber et al. 1959:72). The physical condition of ungulates often reaches a critical level in the most severe or limiting season of the year. Condition indices have been developed that enable the biologist to compare the relative changes in condition over the seasons, and between the sexes, age classes, and populations. Moen (1973) and Stoddars et al. (1975) feel that these condition indices can also be used to compare the quality of the range occupied by the different populations.

A variety of condition indices have been developed, including subjective visual estimates of condition (Leopold et al. 1951), bone marrow condition (Cheatum 1949), antler growth (Park and Day 1952), length-weight ratios (Bandy et al. 1956 and Taber and Dasmann 1958), the kidney-fat index (Riney 1955), and others.

In this study, the kidney-fat index seems to have been the most responsive to changes in condition. The length-weight ratios showed no clear seasonal trend, most likely due to the lack of a sufficient sample size. The bone marrow technique was best suited to indicate the degree of malnutrition in the cases of natural morality.

The results of the kidney-fat index analysis are shown in Figure 27, and in Tables 8 and 9. The data are separated by sex and the reproductive status of the individual. The data from the juveniles, which are in the processing of growing, are not plotted in the figure. While this data does not allow detailed statistical analysis, the following generalizations can be made:

1. The seasonal condition of males is less variable throughout the year than is the condition of the females.

2. The seasonal condition of both sexes increases during the summer and early fall, and declines during the winter and spring.

3. The overall condition of the males is lower than that of the females.

4. Nonpregnant females are in poorer condition than the pregnant females.

5. The non-territorial males are in better condition than the territorial males throughout the entire year.

The interpretation of these results will be more readily understandable after the discussion of the social structure of the guanaco. In general, the condition level of any category of guanacos reflects their ability to obtain access to the food resources, and their physiological demands for growth and reproduction. Thus,

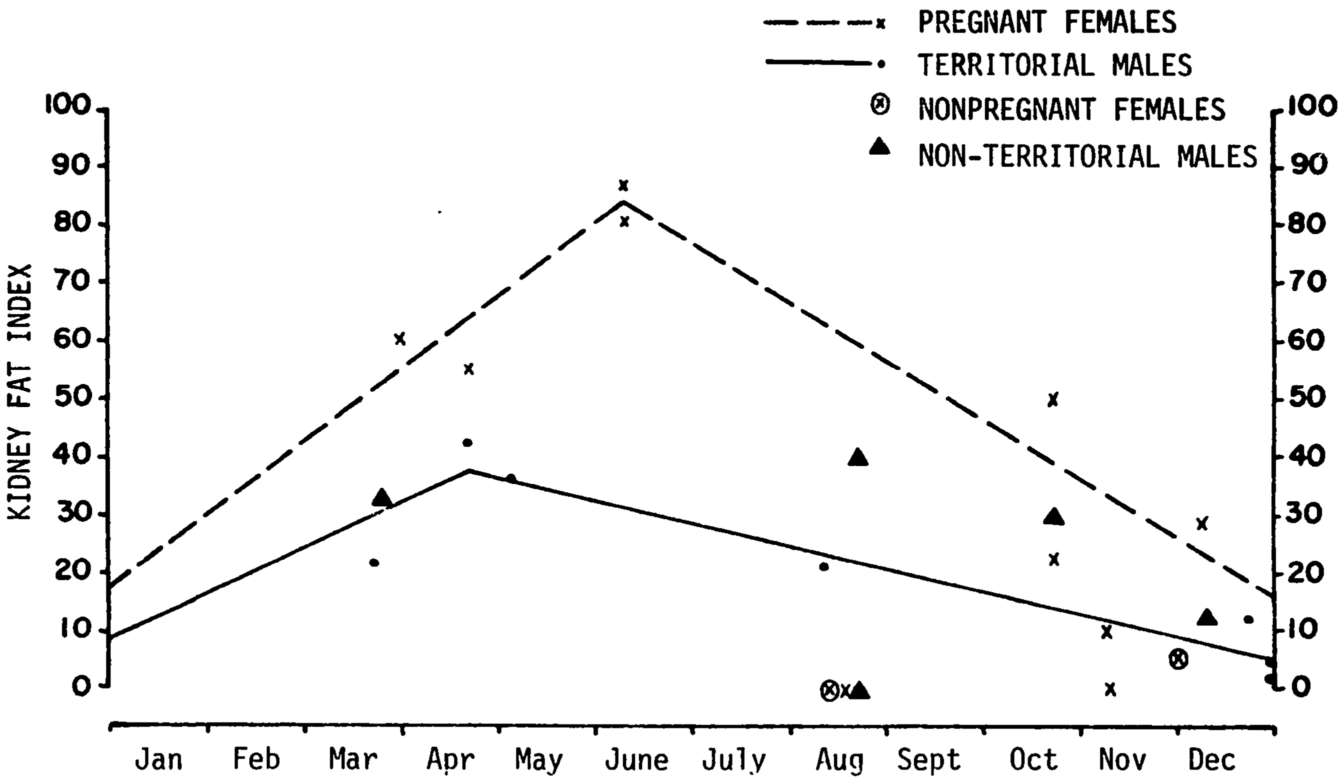

Figure 27. Condition indices for the various classes of guanacos by month, from Isla Grande, Chile (1972-1975).

Table 8. Condition indices for male guanacos from Isla Grande, Chile (1972-1975).

Number	Date	Age	Territorial	Kidney-fat Index	Length-weight ratio
G1	8/72	±7½	Yes	24.4	1.56
G6	12/72	6	Yes	3.2	2.18
G8	3/73	3½	No	21.3	1.66
G9	4/73	8½	Yes	41.6	1.31
G12	8/73	2½	No	41.4	1.52
G13	8/73	6½	No?	0.0	1.64
IDP1	2/74	3	Yes	-	1.69
IDP2	2/74	4	No	-	1.67
G14	5/74	7½	Yes	36.1	1.65
G20	10/74	7½	No	31.0	1.62
G23	12/74	1	No	13.4	1.65
G24	12/74	11	Yes	5.6	1.62

females, which in general have access to the best forage resource, regain condition rapidly in summer. However, they rapidly lose in condition with the heavy demands of the last months of pregnancy and lactation. Non-territorial males are limited to the marginal parts of the range due to exclusion by territorial males, and hence their condition is generally lower than that of the females. Conversely, the territorial males have access to the better forage areas, but are subject to the constant drain of territorial defense and reproduction.

Table 9. Condition indices for female guanacos from Isla Grande, Chile (1972-1975).

Number	Date	Age	Pregnant ?	Kidney-fat Index	Length-weight ratio
G2	8/72	7½	No	0.0	1.45
G3	9/72	9 mo.	No	29.9	2.01
G4	11/72	6½	Yes	0.0	1.53
G5	11/72	8½	Yes	10.1	1.53
G7	3/73	6½	Yes	61.2	1.45
G10	4/73	3½	Yes	56.7	1.49
G11	8/73	8½	No	0.0	-
G15	6/74	17½	Yes	86.5	1.41
G16	6/74	6 mo.	No	102.5	2.12
G17	6/74	1½	Yes	80.0	1.54
G18	10/74	7½	Yes	24.4	1.90
G19	10/74	4½	Yes	52.3	1.63
G21	11/74	3½	No	5.3	1.72
G22	12/74	7½	Yes	29.9	1.67

While these conclusions seem to fit the general pattern of condition, more work needs to be done on the cycle of condition and its relationship to range quality and behavior.

Unfortunately, no comparisons can yet be made with other guanaco populations, since no data exist. When such data have been obtained we should be able to evaluate different management techniques on the basis of condition of the animals in the populations, in addition to demographic vigor.

CHAPTER 6

Behavioral Ecology of the Guanaco

Recent studies have demonstrated that the behavioral patterns of a species have evolved in response to the total environment, and are an important aspect of the ecology of the species (Geist 1971, Wilson 1975, and Barash 1977). Behavior has been shown to influence such basic aspects of a species life history strategies as species distribution (Krebs 1971, Wilson 1975), population density (Orians and Willson 1964), sex of offspring (Trivers and Willard 1973), and even the sex of the individual at different times (Robertson 1972). In addition, it has long been recognized that behavioral interactions are an important factor in competition for access to resources, both at the intraspecific and interspecific levels. Behavior, then is a powerful mechanism in population regulation (see Wilson 1975, and Barash 1977 for a review of this and general aspects of the importance of behavior in the life histories of animals).

In the following sections, a general description of the behavioral ecology of the guanaco will be given. While a detailed study of the behavioral organization of the guanaco was not a major part of this study, numerous observations were made on behavior and its part in guanaco biology.

Before the behavior of the guanaco is described and discussed, several comments need to be made. First, as was mentioned in the previous chapter there are two distinct sub-populations of guanacos found in the study area, migratory and non-migratory. These two sub-populations have responded to their environments in different manners, and their behavioral patterns are often different. Hence, the two populations will be treated separately when they differ, but where they are similar, they will be treated together. Second, most of the literature on the behavior of the South American camels is based on studies of populations at relatively high densities. Koford's (1957) study was conducted in Peru before the vicuna population was drastically reduced, and

Franklin (1978) studied a vicuna population in a reserve where it had recovered under intensive protection. Other literature is often based on observations from the early 1900's when numbers of lamoids were much higher than today (see Chapter 4 for a summary of this decline in numbers). Apparently as a result of the reduced densities, some of the behavioral traits of the guanaco have changed, and new patterns may be evolving. The changes presumably due to a reduction in density will be noted in the following discussions.

6.1 Social Groups

There are three principal types of social groups in the guanaco population: family bands, male troops, and solitary males. Each of these groups has distinct behavioral strategies, which will be summarized in the following sections.

6.1.1 Family Bands

The family bandd is the center of the guanaco social system. The ban contains a single adult (alpha) male and his harem of females and their young of the year. The average band is made up of 5 to 6 adult females (mean of 5.5 with a standard deviation of 3.76, based on a sample of 321 groups, with 1765 individuals), 1 or 2 yearlings, and the young of the year (chulengos). The number of sub-adults (yearlings plus young) varies seasonally throughout the year. A small, but fairly typical family band is shown in Figure 28. The largest band observed

Figure 28. A small family band in the parklands vegetation association of Isla Grande, Chile.

contained 25 guanacos one male, 18 females (including yearling females), and five chulengos. It was observed in the Russfin valley on April 8, 1972. While the number of sub-adults in the band varies over the year, the number of adult females in the band does not change from season to season (see Table 10).

Each family band occupies a territory which the male defends against all other guanacos. The degree of overt territorality is related to the relative density of the guanacos in the area. Where density is high, territorial

Table 10. The number of adult females in the family bands on Isla Grande, Chile (1972-1975).

Date	Mean	95% C.I.	Sample Size
4-72	10.5	± 3.1	9
6-72	7.4	± 2.2	20
7-72	6.5	± 2.0	24
12-72	7.0	± 2.6	23
3-73	6.4	± 2.9	36
5-73	6.5	± 2.7	21
10-73	7.6	± 2.2	13
12-73	6.4	± 1.4	25
5-74	6.0	± 0.7	38
9-74	5.9	± 1.7	23
10-74	5.4	± 1.3	36
12-74	5.8	± 0.5	15

defense is frequent. In all cases, the family bands occupy the best habitats available, generally the valley bottoms, near adequate escape cover.

The family band males are fully mature. The average age of the band males from the wild population averaged 8.0 years, based on a sample of 6 with ages of 7.5, 6.0, 8.5, 7.5, 7.5, and 11.0. The family band males made up only 18% of the males in the population as a whole, as shown by demographic and herd composition studies. The remaining males were found in the male troops, or as solitary males.

The composition of the family band is not rigidly fixed. Changes in band composition were much more common in guanacos that was observed by Koford (1957) for vicuna. Most changes in band composition were the result of the loss or addition of a single female and her young. For example, from June 18 to 21, 1972 the following groups were observed on a flat ridge top along the head of the Rio MacClelland, about two kilometers upstream from the mouth: 5(1,2,2) 7(1,3,3) and 9(1,5,3), where group composition is total(adult males, adult females, juveniles). On June 22, a female and young from the band of 5 had joined the band of 7, which now totaled 9. A week later the new band of 9 was again reduced to 7. The female and young appeared to have departed from the area at this time, and her original band remained as 3 individuals. Whether the same female and young were involved in both moves is not known. However, Koford (1957) found that the last vicuna to join a band was often the next to leave the band, even though it may have remained in the band for some days. The changes in composition of a large territorial band observed in the Russfin valley over a period of 8 months is given in Table 11. The band was easily recognizable since it occupied the same territory over the entire time period.

Table 11. Observed changes in composition of a large territorial band in the Russfin Valley.

DATE	GROUP COMPOSITION	CHANGES IN COMPOSITION
3 May 1974	12(1, 8,-,3)	
5 Sep 1974	16(1,12,-,3)	+ 4 Adult females
25 Nov 1974	16(1,11,-,4)	- 1 Adult female, + 1 Chulengo
26 Nov 1974	16(1,11,-,4)	
4 Dec 1974	18(1,13,-,4)	+ 2 Adult females
8 Dec 1974	15(1,10,-,4)	- 3 Adult females
19 Dec 1974	17(1,12,3,1)	+ 2 Adult females, 1 chulengo born - 1 Yearling female

Many of the changes in band composition were caused by disturbances. Sheepherders and their dogs traveling through a region cause the guanacos to flee for cover. Often small bands will join in flight, or a large band will split in the confusion. In most cases, the original bands will reform, but changes in composition of the bands after such disturbances have been observed.

Territorial band males were observed to limit band size in two ways. First, after the "optimal" band size had been reached, the male would attempt to prevent unattached females from joining the band. Second, the juvenile males of the band were expelled once they had reached an age when they could survive without further parental investment. This would be advantageous for the male if the territories were fixed, resulting in a fixed amount of forage available for the band. The optimum band size would then be related to the size and forage production of the territory. Franklin (1978), working with vicunas, found that there was a significant positive correlation between band size, territory size, and total forage available within the territory. Examples of males limiting band size will be given below.

On August 8, 1972 two female guanacos approached a family band of nine (1 male, five females, and three chulengos). When the two females approached to within 20 meters, the male chased after them, and they fled with the male in pursuit. They all disappeared from sight over a ridge about 500 meters to the north. After about 15 minutes, the male returned to the band, which had continued to graze during most of the encounter. Similar interactions were observed throughout the study period.

The same pattern was not observed in smaller bands containing only 1 to 3 females. These bands showed a considerable amount of fluctuation in size and composition over a period of weeks, as females entered and left these groups. However, in situations of high density, and fixed territorial bounds, the addition of females to even small bands would be less likely, due to the limited resources of the territory.

Band males also limited their band size by expelling their male offspring. The juvenile males were forced from the band between the ages of 6 and 12 months, and most had been expelled by 9 months of age. Franklin (1974) found that in vicuna the mother determined the exact time when the young were expelled. If she was physically protective of her young, she could delay the expulsion. However, as the seasons progressed, the mother-young bond would weaken, and finally she would not defend her young, and the male would drive the young male from the band. Indirect evidence suggests this to be the case in guanacos also. For example, females that were not pregnant the succeeding year were seen to defend their young of the year from explusion, and occasion even young males remained in the band until they were over a year old. On March 12, 1975 a yearling male was observed to nurse for a few seconds as the mother grazed. She was not accompanied by a new born chulengo, and did not appear to be pregnant. However, juveniles males of over 14 months were never observed in an undisturbed family band.

Yearling females are present in many family bands, and apparently are generally not expelled from the band by the male. The data from the studies of population dynamics and herd composition in particular, indicate that the number of juvenile females (1 to 2 years of age) in the family band is predictable as a function of survival rates of the juveniles. Herd composition counts in March and April averaged from 20 to 24 yearling females (15 months old) per 100 adult females in the family bands. This is compared to an expected 26 yearling females per 100 adult females in the bands based on survivorship data (see Chapter 7 on the population dynamics). These calculations indicate that the percent of yearling females that dispersed from the bands varied from a maximum of 23% to a minimum of 8%. However, it is possible that yearling females were sometimes expelled from the family bands, and were subsequently accepted into other bands. If this were generally true, then we would expect to see family bands with more yearlings than adults, or bands of all yearlings and an adult male. Both of these types of bands were observed by Koford (1957) in vicuna populations, but were not observed in guanacos in the present study. Therefore, I conclude that the yearling females ordinarly remained in their maternal bands.

There are several possible hypotheses concerning the question of why males do not expel their female offspring, as do vicuna. First, female vicuna seldom successfully breed as yearlings (Koford 1957, and Franklin 1974) and thus would contribute little to the reproductive output of the band, while they would consume forage resources that could be consumed by reproductive females. However, in guanacos, an estimated 33% of the yearling females reproduce, which is about half the rate of the adult females. Thus the yearling females would contribute significantly to the reproductive output of the band, and thus increse the reproductive fitness of the band male.

at the same time, they would replace natural mortality of the adult females.

Second, since the guanacos observed in this study occur generally a low population densities, and territories often appear to be only vaguely defined, band size may not be highly correlated to territory size or forage availability on the territory. This hypothesis could be tested through observations of social organization in an area with high densities, and fixed territories.

Earlier authors (Housse 1930, Stassen 1916, and others) have repeated the statment that if the family band male was shot, the females of the band remained with the carcass. This was not observed in the present study. When a family member was shot, the other members of the band fled without regard for the killed member. Females also did not actively defend their young, but rather relied on flight to avoid danger. If a chulengo was captured, the mother would remain within 75 to 100 meters, and would vocalize, but would not defend the young.

6.1.2 Male Troops

As in the vicuna, the males that are not part of a family band form male troops. Barros (1963) wrote that these troops were led by a single leader, but this has not been observed in this, or other studies. Troops varied in size from several guanacos to an observed maximum of 60 individuals, including 15 juveniles. This troop was observed in September, when the yearling males had generally left the family bands. Koford (1957) found that the male vicuna troops reached a maximum at this time of the year. However, due to the tremendous variance in guanaco troop size, the data from the present study failed to show any statistically significant ($P=0.05$) seasonal pattern. The male troop fluctuated almost continually with regard to composition and size. Troops numbering 25 to 35 were common throughout the study area, but the norm was closer to 15 or 20. Figure 29 shows a typical male troop. The troop is apparently an open society, which members can join and leave with little reaction from other troop members. Most changes occured through the addition or depature of small bands of 3 to 5 individuals.

When guanaco population densities are high, the male troops are excluded from the prime habitats by the family bands. The male troops are then foreced to occupy the

Figure 29. Part of a large male troop in the parklands vegetation.

marginal habitat at the periphey. This pattern is seen in the Russfin valley, just north of the section Russfin. In this valley, the overall guanaco density is consistantly high, since the area is good range, with excellent forage on the river plains, water, and forest cover nearby. Male troops are noticeably absent from the area when family bands are present. Any male troops seen are generally transient. Male troops that do enter the area are generally chased from the valley bottom. On two occasions, male troops of 5 and 8 members were chased by the family band males to the west to areas unoccupied by the family bands. In Table 13 the composition of the guanaco groups in the valley is given for a period of several months. The percentage of males observed is well below that expected if the guanacos were distributed throughout the area at random.

Over most of the present guanaco range, however, guanaco densities are so reduced that male troops can occupy adequate habitat without fear of being expelled by family males. The herd composition counts, and the study of distribution patterns, show that at low population densities the male troops and family bands are commonly interspersed on seemingly homogeneous range. It is possible that there were microhabitat differences, and that the males were occupying marginal habitat. However, this seems unlikely since both types of groups regularly shifted grazing areas, and an area used by a family band one day might be used by a male troop on succeeding days, and vice versa.

When not harrassed by males from family bands, the male troops usually grazed undisturbed in a single vicinity for some time. For example, a yearling male from a troop of 35 males was tagged in October 1974. Over the next six months he was observed within an area of approximately two square kilometers. During this time, only one encounter with a family band was observed. The male troop was attacked by a band male, where upon it split into two groups which fled from the band male. The family band continued grazing through the area, and departed the next day. The the following day the male troop was observed on the same area where the encounter had occured.

Male troops are most readily identified by behavioral characteristics. The male troop members engage in almost constant play-fighting, chasing, neck-wrestling, and biting. It is generally the yearlings and juveniles that are engaged in the "play" and the older males generally ignore the activities, unless the playful individuals get too close. If a troop member is approached too closely, and does not engage in play, he will often spit and kick at the offender. This is also common among the females in the family bands.

On several occasions, juvenile females were observed in male troops. On May 6, 1974 at least two females, both about one and a half years old were seen in a male troop of 17 guanacos. The closest family band was about 500 meters away. The males in the troop paid little special attention to these females, and all grazed quietly. When they were finally disturbed by the vehicle, they all fled as a group. It is possible that these females had recently left their family band and had temporarily joined the male troop.

6.1.3 Solitary Males

Many of the physically and sexually mature males were observed on the range as solitary males. Franklin (1974) concluded that vicuna males leave the troop to look for an unoccupied suitable site to establish a territory. He reported (Franklin 1975) that only 0.2% in 1968 and 1.1% in 1971 of the vicuna censused were solitary males. Koford (1957) did not recognize these solitary males as a class, presumably due to their low frequency in the population. Neither of these authors reported any seasonal trends in the occurance of solitary males.

In the present study, in contrast to these findings in the vicuna, the average annual percentage of males observed as solitary individuals was 14.5% (or about 8% of the total population). Further, there was a marked seasonal trend, significant at $P=0.05$, in the occurance of solitary males. Figure 30 plots the monthly percentage of all males that were observed as solitary. There is a distinct tendency for a male to separate from the male troop just prior to the onset of the breeding season,

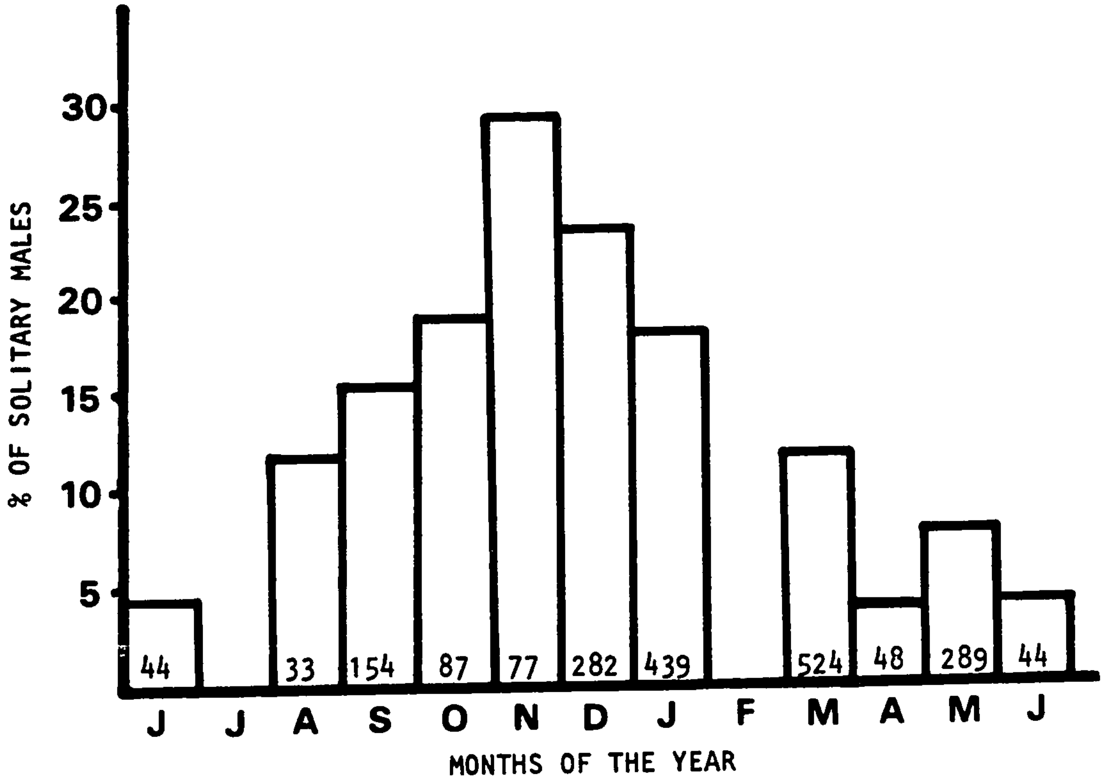

Figure 30. Monthly percentage of male guanacos observed as solitary in the intensive study area, Isla Grande (1972-1975).

which occurs from mid December through the middle of March. The percentage of solitary males was lowest in mid-winter and July. Table 12 summarizes the data, and given the appropriate confidence intervals for the monthly samples.

Why solitary males are relatively more numerous in guanaco populations than in vicuna populations is most likely due to the more fluid social organization of the guanaco, and the reduced density of guanacos on the range.

Table 12. The percentages of male guanacos observed as solitary males. Presented by month with the 95% confidence intervals.

Month	Total Males	Solo Males	% Solo	95% C.I.
January	439	80	18.2	(14 - 22)
February	-	-	-	-
March	524	64	12.2	(10 - 15)
April	48	2	4.2	(1 - 12)
May	289	22	7.6	(5 - 12)
June	44	2	4.5	(1 - 15)
July	-	-	-	-
August	33	4	12.1	(5 - 28)
September	154	24	15.6	(9 - 22)
October	87	10	18.7	(13 - 26)
November	77	22	28.5	(17 - 42)
December	282	66	23.4	(18 - 28)
TOTAL	2257	362	16.0	(15 - 17)

With reduced densities, suitable territorial sites are not as limited as is seemingly the case for vicuna, rather, females are the limited resources. Hence, with the considerable movement of females between bands, and suitable sites available, more males would be likely to leave the male troops, and attempt to form a family band. Since these lone males would not have to engage in fighting for the sites, as they are unoccupied, their only cost is the lost protection from predators that group membership reportedly confers (Altmann 1974).

These data indicate that the solitary males are beta males, most dominant in the male troops and fully sexually mature, yet unsuccessful in ousting territorial (alpha) males. These males separate from the troop prior to mating, and attempt to establish territories and secure mates. If unsuccessful, many return to the male troops until the following mating season.

6.2 Territoriality

A territory has been defined as "an area occupied more or less exclusively by an animal or a group of animals by means of repulsion through overt defense or advertisement" (Wilson 1975:256). Territorality is adaptive when there is competition between individuals for a limited resource which is defendable (Brown 1964). Resources most often cited as being defended within a territory are food, nest or den sites, or mating grounds. Wilson (1975) reviews the examples of territorality in which the primary function is known.

Koford (1957) was the first to describe territorial behavior in South American camels, in his study of the vicuna in Peru. He found that a resident male vicuna defends the home range of his band; that is he drives of males from the area in which his band normally grazes, rests, and cares for their young. Barring disturbances, the band normally remains on their territory. However, a band may be driven from it's territory by disturbance, later returning. Koford hypothesized that the function of the territory was to defend an adequate food supply for the band.

Territoriality has presumably evolved to maximize the increment to fitness from the energy resources utilized from the defended area, at a cost of defense in energy, exposure to predation, less time for courtship, neglected offspring, reduced foraging time, etc. (Wilson 1975). Hence territorial behavior is a function of the parameters of food distribution and abundance, predation, and density of conspecifics. Changes in these parameters affects the net benefits of the territorial strategy.

In the guanaco population of Isla Grande, the distribution and abundance of the food resource have been considered to be the most important factors affecting life history strategies (Raedeke 1978). In response to the differences in the food resource, two distinct territorial strategies have been observed: spatiotemporal territories in areas of low guanaco densities on poor range, occupied by migratory populations, and second, the more classical territoriality as in the vicuna, in areas of higher density on the more productive ranges. These two models of territoriality will be described below.

6.2.1 Fixed Territories

On the most productive range areas, where guanaco densities are at their highest, the social organization and territorial behavior of the the guanaco parallels that of the vicuna as described by Koford (1957). The principal difference between the two species is that the guanaco social system is more fluid, with greater exchange between family bands, and more frequent changes in territorial borders, and occupation of territories.

The best example of the territory of Type A, (Wilson 1975) where courting, breeding, feeding, and resting all occur on the same territory was observed in the Russfin valley, two kilometers west of Russfin section. The valley is approximately 900 meters wide, bisected by a creek, and with beech forest on the rolling hills on the north and south sides. The area between the creek and the woods on the north was occupied by territorial family bands throughout the year. For example, on 23 October 1973 the following bands occupied territories:

13(1,9,0,3), 1(1,0,0,0), 6(1,4,,0,1), 3(1,1,0,1), and 6(1,5,0,0). These family bands were spaced almost exactly one kilometer apart in the area between the creek and the woods, on the opposite side of the creek from the road. The solitary male occupied a roughly triangular territory between two family bands on two sides, and the woods on the third. All territories were roughly 250 to 300 hectares in area; however, the bounds between the family bands were not precisely determined since few group interactions were observed. No fights between the family band males were observed. However, the two family band males, and the solitary male with abbutting territories spent 25% of their time between the hours of 1400 and 1600 hours (the observation time) in displays along mutual borders. Meanwhile the females of these bands spent the entire time grazing (60%), and resting and ruminating (40%). On 24 October 1973 the same family bands were observed in the same positions. On 25 October 1974 the band of three was not observed, and its territory was unoccupied. The other bands were in the same locations- i.e. they had not expanded to occupy the vacated territory.

The number and composition of the groups that occupied territories in the valley varied greatly over time. Table 13 summarizes the observations of the groups

Table 13. Guanaco family groups observed in the Russfin Valley, Isla Grande. The observations were made over five months.

Date	Group Composition
25 Nov 1974	8(?)
	16(1,11,0,4)
	7(1, 5,0,1)
	1(1, 0,0,0)
26 Nov 1974	3(3, 0,0,0)
	7(1, 5,0,1)
	7(1, 4,0,2)
	3(1, 2,0,0)
	1(1, 0,0,0)
	16(1,11,0,4)
	5(1, 3,0,1)
4 Dec 1974	1(1, 0,0,0)
	7(1, 6,0,0)
	18(1,13,0,4)
	12(1, 8,0,3)
8 Dec 1974	7(1, 4,0,2)
	5(1, 4,0,0)
	1(1, 0,0,0)
	15(1,10,0,4)
19 Dec 1974	17(1,12,3,1)
	1(1, 0,0,0)
	1(1, 0,0,0)
	9(1, 6,2,0)
20 Dec 1974	2(2, 0,0,0)
	10(1, 6,2,1)
21 Dec 1974	4(1, 2,1,0)
	12(1, 8,2,1)
	2(2, 0,0,0)
	7(1, 4,1,1)
27 Dec 1974	1(1, 0,0,0)
	10(1, 7,2,0)
24 Jan 1975	1(1, 0,0,0)
	23(1,14,5,3)
	4(1, 1,0,2)
	2(2, 0,0,0)
27 Jan 1975	22(1,14,3,4)
	1(1, 0,0,0)
11 Mar 1975	1(1, 0,0,0)
	4(1, 2,0,1)
	1(1, 0,0,0)
	10(1, 6,2,1)
	5(1, 2,1,1)
12 Mar 1975	4(1, 2,0,1)
	10(1, 9,0,0)
	4(?)
	1(1, 0,0,0)
	9(1, 6,0,2)
	1(1, 0,0,0)
	10(1, 6,2,1)
	5(5, 0,0,0)
	13(1,10,0,2)

in the valley over a 5 month period. Few groups could be readily identified by composition or location over a period of time exceeding several months. One large group, occupying the better area in the valley, was observed from May through December 1974, and the changes in composition of this group were given in Table 11.

The territory of the family bands did not include the sleeping areas. Generally, guanacos retreat to cover, such as the forest, for sleeping at night, and return to the feeding grounds in the morning. The sleeping cover also serves as escape cover when the band is disturbed. Most territories, such as those in the Russfin valley, were bounded by forest on at least one side. Whether various bands sleep in close proximity as observed in the vicuna (Koford 1957) is not known.

Band males defend their territory, and establish the borders through aggressive encounters and displays. Males of family bands are intolerant of any males in their territory except for their own young of the year, and will attack any male that violates the borders. Most of the encounters observed during the study were between territorial males and troop males. The family band male would attack and chase troops when they approached to within 20 to 50 meters of the band. The male troop always fled from the territorial male, which might pursue them several hundred meters beyond the borders of his territory. On one ocasion, a male chased a troop of 14 males for approximately 600 meters beyond the border of his territory before returning. When these encounters take place, the females of the band generally continue to graze, or rest, and take little apparent notice.

The encounters between band males generally occurred along the mutual borders, and were mostly restricted to aggressive displays. As in the vicuna, the male guanaco displays seemed intended to make the male appear as large as possible. The male would stand on any available relief, with his neck and tail erect, and display broadside to the other male.

Actual fighting between males occurs most often between family band males and solitary males, especially in November and December, just before the breeding season. When fighting, the males rear on their hind legs and kick, neck wrestle, and attempt to bite the opponent on the neck and force him to his knees. The bites inflicted on the neck and legs often result in serious wounds. An eleven year-old male was collected from a family band in December. He had 78 visible scars from fighting, distributed on the front of the hind legs (13), inner front legs (17), back of the front legs (15), the front of the hind legs (11), and the back of the hind legs (22). Several of the wounds were fresh, and were not yet healed over. Males collected in months other than November through January usually did not have fresh cuts or wounds. The high incidence of fighting between males coincided with the peak in breeding and also when solitary males were most frequently observed on the range.

Males can gain a territory and a band of females either by combat with a band male, by taking over a band in which the male has become incapacitated or killed, or more commonly by defense of a territory at the perimeter of the prime habitat occupied by family bands and acquiring females that are not attached to a band. Since individual guanacos are virtually impossible to distinguish, without tagged animals, it was impossible to note changes in the individuals within the groups, other than quantitatively, unless the change was observed. Hence, little data was collected on the changes in the composition in family bands. However, on one occasion, a band male was collected from his band of 6 adult females, and 3 chulengos. He appeared to be replaced by another male within two days, without loss or dispersal of the band. Koford (1957) noted that in vicuna when a territorial male became injured or removed from the territory, the band dispersed or was taken over by a new male.

Territorial band males did not defend their territory against the other ungulates of the study area, all of which were domestic livestock. Unlike vicuna which fled from their territories when livestock or domestic llamas or alpacas intruded and did not return until the stock had departed (Koford 1957), the guanaco were only temporaily displaced by such encounters. Unless the livestock were accompanied by herders and dogs, the guanaco were quite tolerent of the intruders. With stock present on the territory, the territorial band would shift their center of use to a different part of the territory. However, if the stock were sheep in great numbers, the constant disturbance of the sheep, and especially the herders and their dogs would finally displace the guanacos. Displaced bands generally attempted to establish new territories in suitable habitat outside the area of disturbance, often in an adjoining pasture without stock. Many of the changes in groups and group composition observed in the Russfin valley, and summarized in Table 13 resulted from the movement of stock into the area, or stock in transit to the Russfin shearing sheds and sheep baths.

6.2.2 Spatiotemporal Territories

The migratory guanacos of the southern part of the study area (see Figure 17), and the guanacos in areas of low guanaco density, did not defend fixed territories as described in the previous section. Rather, these two populations defended the areas that they happened to be in at the moment. The reasons for this behavior are quite distinct for the two populations, and will be addressed separately.

6.2.2.1 Spatiotemporal Territories: Low Density Populations

If the function of territorial behavior in guanacos is to secure an adequate food supply for the band, we would expect changes in the food distribution and abundance to modify territorial behavior. In areas of high productivity, territories would be small, with readily observed and defended borders. This was found to be the case with fixed territories, as described in the previous section. However, when the range production is low, the territories must be large, and would have extensive, vague borders which could not be watched all the time, and so could not be defended. For example, if on highly productive range one square meter of range will support a guanaco, it must then defend 4 meters of border. But if it takes four square meters of poor range to support a guanaco, then it must defend 8 meters of border, and so on. After a point, territorial defense is no longer enegetically feasible.

In areas of lower guanaco population density, the family bands were cohesive, but nomadic within large areas, and did not defend the entire area in which they foraged, courted, or bred. Instead of fixed territory occupied day after day, with definite borders, these guanacos occupied a large home range, and defended only the area immediately suppounding the band. The area defended often varied over time, and was used by several band consecutively.

For example, on several occasions family bands were observed to defend a territory in one area one day, and several days later, a new band would be territorial in that same location. In January 1973, two family bands, with compositions of 9(1,4,1,3) and 14(1,8,2,3) were observed feeding 250 to 300 meters apart on the open pampa in a parklands area near the section Rio Grande. This area is sheep winter range, and had not yet been grazed. However, the forage was only moderately abundant in the area. Each band contained one individually identifiable tagged chulengo. Over a period of January 6 to 9, 1973, these two bands were observed to maintain a minimum distance of 200 meters between the bands, and the band males generally grazed or displayed in the area separating the bands. During the period of observation, the two bands exchanged feeding sites two times and much of their feeding occurred in mutually utilized areas. When disturbed, the bands often mixed in flight. However, group composition remained unchanged on successive days when they were undisturbed.

There are several possible explanations for the evolution of the this type of territorial strategy.

First, "natural selection theory, predicts that an animal should protect (defend) only the amount of terrain for which defense gains more energy than it expends" (Wilson 1975:268). Hence if the resource is evenly distributed, but in reduced amounts, the costs of expelling an intruder from a territory sufficiently large to support the band may be an energetically wasteful activity. The resource may not be economically defensible.

Second, at low population densities, territorial defense may be mute or suspended since it may not be necessary. In the previous example, the forage resource may not have been limiting at the time for this density of guanacos, or territorial borders may not have been established since the lack of intruders has obviated the need for the establishment of borders. Koford (1957) showed that the territorial borders were established and maintained in response to repeated incursions and forays by neighboring males. These interactions not only establishthe borders, but also continually tested them.

Third, the forage resource in the areas of reduced guanaco densiities may not be defensible, since the resource is patchy in time. Fixed territories were observed only in areas with resources that were more continuously renewed, such as in the valley bottoms with an adequate supply of moisture for continued plant growth. In the areas of low guanaco density, the forage was patchy over time, since growth was limited to the period of spring moisture, and the availability of the forage varied with the changes in sheep movements. Horn (1968) showed that under such conditions, feeding areas are generally not defended, since the distribution of the resource is not predictable.

6.2.2.2 Spatiotemporal Territories: Migratory Populations

The guanacos of the southern part of the study area migrate seasonally following the spring appearance of new growth as the snow retreats up the precordillera. The basic social organization of this sub-poulation is similar to that of the other guanaco population in most regards: family bands, each with a single male, male troops, and solitary males were all observed as in the resident populations. The juvenile males were expelled from the family bands. However, due to the migratory movements, the defense of fixed territories was not possible.

Territorial behavior of the migratory guanacos appeared to be similar to that of the non-migratory guanacos found at low densities. A spatiotemporal territory surrounding the band was defended against other family bands, and male troops. Displays and aggressive encounters were observed on the winter range. However, on the summer range, the guanacos were so dispersed that no encounters were observed.

The territorial strategy of the migratory guanacos apparently evolved in response to two characteristics of the forage resource: first, animals are committed to floating or spatiotemporal territories when the resource on which they depend is mobile. While the forage resource of the guanaco is not mobile per se, its abundance changes as the snow retreats in the spring, and the plants begin new growth. As the spring progresses, the guanacos must shift their territories up hill, following the new spring plant growth. These movements take the guanacos from the winter range, which by spring is impoverished, to the summer range where forage is superabundant. Fixed territories are not possible since the most nutritious and abundant forage is in the area of the new growth, which changes with the seasons.

Second, fixed territories would not be adaptive in the summer, since the forage in this time period is not a limiting resource. Without greater densities of guanacos on the summer range, intraspecific competition for forage can not be expect to cause guanacos to be territorial.

6.2.3 The Function Of Territoriality

Many functions have been ascribed to territorial behavior in animals, such as facilitation of breeding, familiarity with the resources (Hinde 1956), reduction of strife, and the prevention of overgrazing (Koford 1957), the prevention of epizootics (Hinde 1956), regulation of population density (Kluijver and Tinbergen 1953, Franklin 1974, and others), and the regulation of population size (Wynne-Edwards 1962). While these may be consequences of territorial behavior, it is likely that they are not the principal selective forces shaping the particularities of territorial behavior (Wilson 1975). Since one objective of the present study is to determine the factors that are limiting the population growth of the guanaco, the role of territoriality in population regulation must be considered.

Wynne-Edwards (1962) and others have argued that territorial behavior has evolved for the "good of the species" as a means of limiting the population to the number that can be supported by the environment as a whole. This requires that the process operates through a "...combination of altruism on the part of the non-breeding nonterritorial animals and/or spite on the part of the territorial holders" (Barash 1977:271). Thus territorial behavior is thought to limit population numbers below the forage carrying capacity and is the ultimate cause of population regulation, rather than resource limitations.

This hypothesis has been proposed for the regulation of the vicuna densities, and ultimately population size, by Franklin (1974:485), who stated that "habitat resources probably dictate group size within the feeding territory, they do not regulate it, the territorial male does."

In response to this hypothesis, Wilson (1975:275) states that "boiled down, the argument turns on whether exclusion regulates the populations, or whether food supply ultimately plays the role...Food supply...is very likely the ultimate factor...Territorial behavior is the mechanism for defending it when it is in short supply. The buffer effect causing population stability is the by-product of territorial behavior...territoriality evolves by selection at the level of the individual."

A considerable amount of evidence is available to support the hypothesis that territorial behavior evolved ultimately to increase individual fitness, rather than to regulate population densities or size. For example, if territories have evolved to regulate populations, individuals would be expected to maintain territories larger than necessary for their own resource needs thereby "reducing the fitness of others, as well as themselves by wasting time and effort in defending space that does not add to their fitness" (Barash 1977:271).

However, territorial systems that have been studied show a high correlation between energetic needs and resources of the territory (Wilson 1975, and Franklin 1978). Furthemore, Koford (1957) observed that territorial males would attempt to mate not only the females in their own bands, but would also seek to copulate with any other receptive females. This can only be interpreted as an attempt by the males to maximize their own fitness, and would negate any speculation that these same males were being altruistic, and attempting to regulate population numbers through behavioral patterns. Other evidence supporting the hypothesis of evolution of territoriality by natural selection at the individual level has been reviewed by Wilson (1975) and Barash (1977).

The conclusion is that territorial behavior is a form of intraspecific competition for the limited resources of the environment, that has evolved through individual selection. As a consequence of this contest competition, territoriality is a proximate mechanism in the regulation of the population density, but resource competition is the ultimate force.

6.3 Defecation-Urination

Unlike the majority of ungulates that defecate and urinate widely throughout their range, the lamoids of South America tend to defecate and urinate in communal piles. Many of these piles have been used year after year, and are quite large; up to three meters in diameter, and 20 to 30 centimeters in depth. Franklin (1974) found that communal dung piles of vicuna have a dry weight of as much as 24 kilograms. In the treeless altiplano, these dung piles are an important source of fuel for cooking and heating for the natives.

Communal piles are used by all members of social groups. On successive days different family bands, and a male troop were all observed to defecate-urinate on the same pile. Koford (1957) found that alpacas and llamas will use vicuna piles for defecation-urination sites also. He also observed that displaced family bands of vicuna will freely use the dung piles on the territories of other bands. The function of dung piles is not well understood. Most authors conclude that communal dung piles are used to mark territory, as in the case of foxes and other canids (Wilson 1975). However, the communal piles do little to keep other conspecifics out. Thus, Franklin (1974) suggests that these piles function to keep the band within its territory, by providing information on the location of territorial boundaries. Part of the basis for this hypothesis is the fact that the altiplano, where he did his work, is rather barren, and lacking in visual markers. However, such is not the case in southern Patagonia, where visual markers on the territories are quite abundant.

The hypothesis of territorial marking by dung piles is supported by the relationship of communal dung piles and guanaco density. At low density, where territorial boundaries are vague of even nonexistent, guanacos tend to defecate widely on the pampas, while at higher densities where territorial behavior is commonly observed, communal piles are almost always used. In an extreme case, three guanacos in a large corral in Punta Arenas used communal piles exclusively, and had rigid territorial borders.

Dung piles also influence the surrounding vegetation and soil development. Koford (1957) and Franklin (1974) both observed that the vicuna fecal piles were surrounded by areas of more luxuriant grass and other plants. On Isla Grande, fecal piles also increased the plant growth in the immediate area. In areas with moderate soil moisture, the area surrounding the dung piles, within several meters, had a greater density of soft succulant grasses and many forbs. However, in the drier areas, the effect on the surrounding vegetation was minimal. With regard to the total production of forage on the range in the study area, the increase due to dung piles was insignificant.

6.4 The Daily Cycle

The guanaco is diurnal, spending most of the day feeding on the pampa, and sleeping during the night in concealment in the forest. The daily cycle varies with the season of the year. In summer, with abundant forage and long days, the guanaco is less hurried, and often begins to feed in mid-morning, several hours after sunrise. In contrast, in the winter with short days and scarse forage, the guanacos often begin to feed before sunrise. Feeding is the main activity of the day.

In the mornings, the guanaco begin the day by feeding in the area where they slept, and gradually work their way out onto the pampa. They feed as they move out onto their territory. By mid-morning the majority of the guanacos can be seen feeding anywhere from the edge of the forest, to several hundred meters out on the pampa. By mid-day, most bands have reached their territory or their main feeding area for the day. These movements between feeding areas and the sleeping sites are as great as 1.5 kilometers, but are usually closer to several hundred meters.

By early afternoon, guanacos are often seen sitting in the typical camel position, with their feet tucked under the body, as they rest or ruminate. Feeding again becomes intense in the late afternoon and early evening. By sunset most of the guanacos retreat to the sleeping areas in cover. Guanacos are seldom seen at night. Franklin (1974) and Koford (1957) both found that vicuna bands formed compact sleeping territories, in close proximity. However, this was not observed in guanacos.

The daily cycle seemed to be affected very little by daily weather conditions. Guanacos were seen grazing on the open range in snow storms, and even hail. However, in the winter, the accumulation of snow on the pampa often restricted the movements of guanacos to the forest areas, where they spent the day browsing on the beech trees and shrubs.

No special movements in search of water were noted in this study. Local lore says that all guanacos make a daily trip to the ocean to drink the salt water; however, this was never observed. Water is freely available through most of the range areas on the study site. In the drier areas of Patagonia, where water sources have been developed for the sheep at great expense, guanacos have been a problem for sheepherders (Howard 1969). Water needs of the guanacos of the study area are probably met by the water content of the forage, and an occasional use of free standing water.

CHAPTER 7

Population Dynamics of The Guanaco

A population is the sum total of all the members of a given species inhabiting a common geographical area at one time. The population has features over and above those of the individual animals, characterisitcs that we have attempted to measure and describe. A population has a density, sex and age-class structure, social organization, natality and mortality rates, etc. All these characteristics change over time, in response to changes in the environment. A population grows, declines, or remains stable. It is dynamic.

An understanding of the dynamics provides a powerful analytic tool, since much of the information which can never be obtained by direct observation can be developed through analytic reconstruction of the population and its working. It is seldom possible to observe all the various characteristics of the population in the field their study requires careful sampling and the use of mathematical analysis.

In the following sections, the different parameters of the population, and the dynamics of the population will be described and analyzed for the guanaco population of the intensive study area. Generally, the discussion will treat only the non-migratory population. However, whenever data are available, the differences between the migratory and non-migratory populations will be analyzed, and described. The first five sections will deal with the raw data of population dynamics: natality, mortality, movements, sex and age structure, and numerical abundance. In the last section, these parameters will be used to develop a model of the the dynamics of the guanaco population.

7.1 Reproductive Ecology of the Guanaco

The ability of an animal population to increase its numbers, or remain stable for that matter, depends on the rate at which new individuals are added to the population through birth and immigration. The reproductive rate of a population depends on the mean litter size, mean number of litters per year, the sex ratio at birth, the age structure of the population, and the population density. Each of these factors is in turn susceptible to modification by environmental factos, such as weather and the nutritional quality of the diet. The ultimate objective of a study of reproduction in population biology is the production of a fecundity table, which integrates all these factors.

7.1.1 The Female Reproductive Life Cycle

Before we can attempt to estimate the fecundity of a population, we need to understand the physiology of reproduction of the species, since much of the information we desire is derived from the interpretation of anatomical structure, and physiological processes.

7.1.1.1 General Anatomy of the Female Reproductive Tract

The study of the reproductive organs of the family Camelidae has remained incomplete, and no literature is available on the reproductive anatomy of the guanaco. However, the reproductive ecology of the alpaca and llama has been studied in some detail, and reviewed by Novoa (1970), England et al. (1969a and 1969b), and Fernandez Baca (1971).

OVARIES. The ovary of the guanaco is ovoid in shape, and is structurally similar to the ovary of the alpaca and llama. Ovaries from non-gravid females averaged 16.5 by 11.7 mm in size. Numerous follicles could seen on the surface of all ovaries, appearing clear or darker than the surrounding ovary, which was a creamy white in color. In adult guanacos (2 years and older) there were up to 30 or more follicles per ovary, most of which had a diameter of less than 3 to 4 mm, with an occasional one or two follicles reaching a diameter of 10 mm or more in non-gravid females. A non-gravid female collected in the end of November, just before the start of the parturition season, had an atritic follicle, 9 mm in diameter, and a second 9 mm follicle still developing, and 5 follicles 5 mm in diameter. These larger graafin follicles were not seen in gravid females. Corpora albicantia from past pregnancies were visible as dark, heavily pigmented reddish-orange structures, up to 4 mm in diameter, but decreasing in size with age.

The shape of the ovaries from gravid females was strongly influenced by the size and position of the corpus luteum. During pregnancy the corpus luteum was a soft, pink colored sphere, almost wholly protruding from the surface of the ovary. Its diameter averaged 16.1 mm.

UTERUS. The uterus of the guanaco is bicornuate, as in all Camelidae (Novoa 1970). The mucous membrane of the cornua and the uterine body are smooth, with no cotyledons. The right cornu is shorter than the left in the llama and alpaca (Novoa 1970).

PLACENTAE. The foetal placenta in the Camelidae is diffuse in nature, and not cotyledonous as in the true-ruminants (Novoa 1970). The placenta is classified as chorioallantoic and epithelio-chorial, similar to the horse. These characters are used to separate the Tylopoda from the Ruminata.

7.1.1.2 Physiology of Reproduction

ESTRUS and OVULATION. The guanaco is multiovular (may pass through several estrus cycles if conception or pseudopregnancy does not occur), with a restricted breeding season in the wild. Circumstantial evidence suggests that the guanaco may be an induced ovulator, as are the other members of the Camelidae (Novoa 1970).

The llama and alpaca ovulate as a result of coital stimulation during the follicular phase (England *et al.* 1969b, Novoa 1970, and Fernandez Baca 1971). After the onset of estrus the female exhibts irregular and unpredictable estrus cycles, with estrus interrupted by irregular periods of diestrus. This same pattern was observed through two breeding years in a guanaco held in a large corral in Punta Arenas. Periods of apparent receptivity were separated by irregular periods varying from 10 to 23 days. Observations were difficult, however, since there was little outward change in appearance or behavioral patterns of the female during estrus, unlike the camel which exhibts swelling and discharge from the vulva, and restlessness. This lack of regular estrus cycle suggests that the guanaco may also be an induced ovulator. However, before an conclusions can be drawn, detailed work on the reproductive physiology of the guanaco is needed.

The reproductive cycle begins with the development of the graafin follicles in non-gravid females, the follicles start to develop as early as August, four months before the start of the breeding season. However, pregnancy appears to inhibit the follicular development, since in the 10 gravid females examined, no developing follicles were observed, even as late as the first week in December.

Guanacos exhibit a "foal heat" 3 to 4 days after parturition, similar to that reported for Asian camels by Asdell (1964). However, copulation during this apparent estrus probably does not result in conception since the uterus most likely has not fully recovered after parturition (Julio Sumar, per. comm.). Furthermore, the lack of mature follicles would also preclude ovulation and conception. Field evidence that these copulations do not result in conception is provided by the observation that births are never observed in November. There is currently no known function for foal heat.

Ovulation in the guanaco appears to be symetric while implantation is asymetric. In the 11 females examined, there was no significant asymetry in ovulation between the right and left ovaries. Zungia (1958) had reported a 12.9% asymetry, in the alpaca, with the right ovary being less active. However, Fernandez Baca <u>et</u> <u>al</u>. (1973) remarked that those results were not statistically significant, and furthermore found that there was no asymetry in their study of 928 females. In the same study, they found that 98.4% of all females had the fetus implanted in the left horn of the uterus. In the present study, 9 of the 11 guanacos examined had the fetus in the left horn. This was significant at the P=0.75 level.

In guanacos there is currently no evidence to support an hypothesis of multiple ovulations. Secondary or auxillary corpora lutea, resulting from ovulations after implantation has occurred, were not observed in the 15 females examined. And while polyovular follicles were observed in three pairs of ovaries out of a total of 15 pairs, multiple implantations were never encountered. Fernandez Baca (1971) found multiple ovulations in 10% of the females studied, but no multiple births in over 12,000 recorded births.

SEASONALITY OF ESTRUS AND PARTURITION. The entire life cycle of the guanaco of southern Patagonia is adapted to the harsh temperate environment. The seasons have imposed an annual cycle of breeding activity, with the young being born in the spring when the weather is mild and forage is most abundant

The observations of breeding behavior indicate that the peak of the breeding season is in February. The earliest copulation observed was on December 30, and the latest was March 15. However, few actual copulations were observed, due in part to a shortage of field days in this season. Without observations of copulation, the breeding season is difficult to delimit, since neither sex exhibits any change in physical appearance during the breeding season. However, if we back date from the birth season, using a gestation period of 11 months, then the peak in breeding is January to March.

The parturition season of the guanacos of Isla Grande is confined to the period from the beginning of December to mid-February. The season of birth was determined through an analysis of the herd composition data from the 1974-1975 season. The percentage of adult females (2 years of age and older) accompanied by new born chulengos was recorded daily throughout the birth season, starting from the first observation of a new-born, on December 6, 1974. The daily observations were then plotted, and Figure 31 gives the results. A logistic function was fitted to the data. The results indicate that by the end

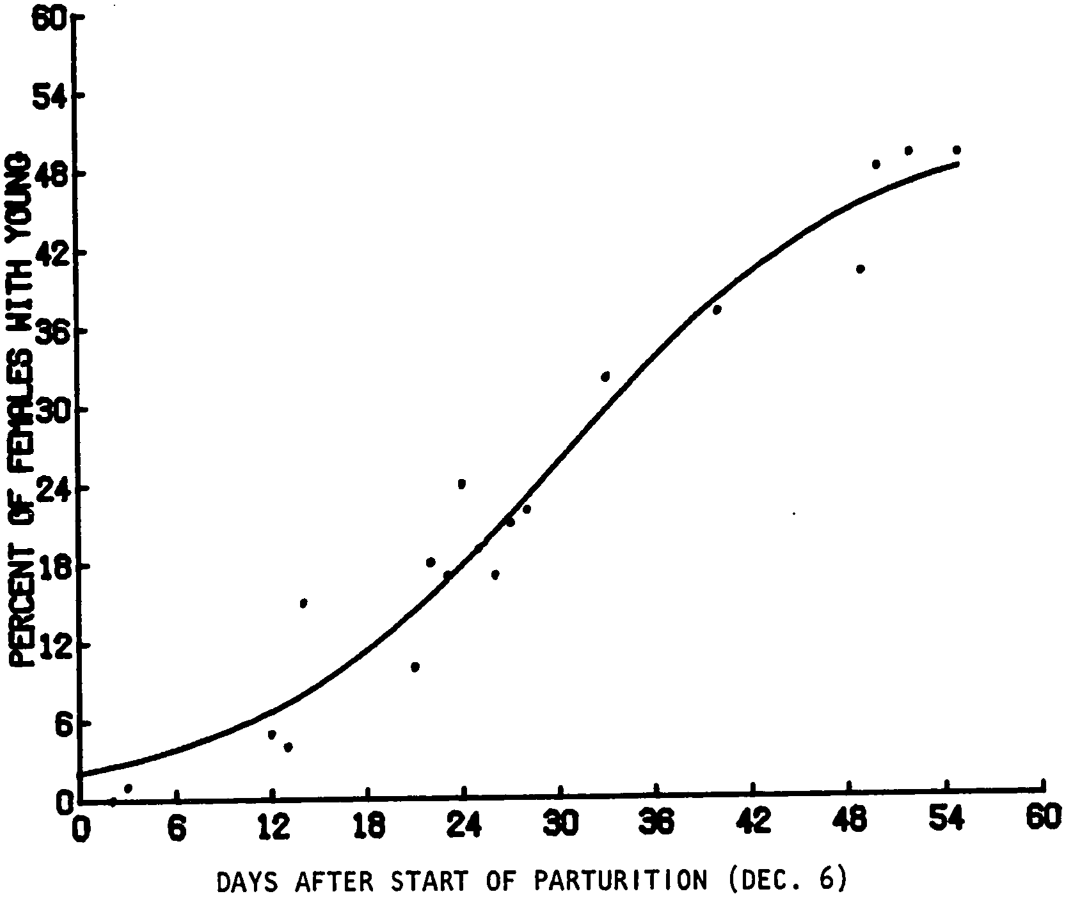

Figure 31. The percentage of adult females observed with young, starting with the first observation on December 6.

of January, tne percantage of adult females with young has reached a plateau, and actually begins to decline slightly after this point, as new births are offset by neo-natal mortality. If we assume a 15% post-natal mortality rate, and a 65% overall reproductive rate (see the later sections of ths chapter for the calculation of these percentages), then fully 90% of the births have taken place in December and January, with 75% occurring from

December 15 to January 20, and the peak being the first week in January.

Throughout the range of the guanaco the birth season corresponds to the season of the year when conditions are most favorable for the survival of the young. The following birth seasons have been observed in different localities: Callpuy, Peru (8 degrees S. Latitude) mid-April to June (Franklin 1975); Patagonia, November (Cabrera and Yepes 1940); Patagonia, approximately 40 degrees S. Latitude, November-December (Simpson 1934); northern hemisphere zoo's, May to August (Schmidt 1973). Other dates have been published, but with no indication as to the location of the observations.

GESTATION PERIOD. The length of the gestation period in the guanaco has been reported as from 10.5 to 11 months (Stassen 1916, Cabrera and Yepes 1940, Cardozo 1954, Novoa 1970, Schmidt 1973, Walker 1975, and others). The observations of the peak in copulations in mid-February, and the peak in births in mid-January, indicate that the gestation length for the guanaco of Isla Grande is approximately 11 months, as reported for the other locations.

EMBRYONIC MORTALITY. Mortality of embryos and fetuses from the implantation stage to parturition appears to be minimal in wild ungulate populations, unless the population is infected with disease causing abortion (Swenson 1973). However, Fernandez Baca et al. (1970) found a significant decrease in alpaca preganancy rates from 70% on day 3 to 35% on days 28 to 31, which they attributed to the embryonic migration from the right horn of the uterus to the left horn. The former appeared to be a less suitable environment for the embryo. Since the guanaco also exhibts aysmetric uterine implantation, this is a potential source of embryonic mortality.

During the present study, no evidence was found to suggest that any significant interuterine mortality occurs in the guanaco. In the 16 females collected, and 12 natural moralities autopsied in the field, no signs of embryonic mortality were observed, even in the latter group which would be most susceptible to fetal resorbtion or abortion, since most had died from starvation. Each corpus luteum observed was matched by a viable fetus. The females that were not pregnant did not appear to have any of the characteristic ovarian structures, such as atretic corpora lutea or hyalin-type ovarian scars, believed to represent embryonic mortality, found by Thomas (1970) in his study of the ovary and reproductive physiology in free-living black-tailed deer.

Since my sample of females in the first 4 months of pregnancy totals only six, the conclusions of insignificant embryonic mortality in the early stages of gestation must be merely tenative.

7.1.2 Sexual Maturity

The age of first breeding, especially for females of polygynous species can profoundly affect the reproductive rates of the population, since the younger age classes typically constitute a large proportion of the total population in ungulates. In general, the likelihood of an ungulate breeding as a yearling is influenced by its rate of maturation, which in turn is affected by its environment.

There is no evidence to suggest that either sex of any lamoids breed during their first summer, i.e. at one to two months of age (Novoa 1970, and Novoa et al. 1972).

Both sexes of guanaco can successfuly reproduce in their second year. In captivity, two yearling males successfully inseminated a yearling female. However, in the free-ranging populations, males under the age of five years are unlikely to obtain access to estrus females due to the highly polygynous mating system.

The reproductive success of yearling females appears to be a function of nutrition. Yearling females maintained on a high plane of nutrition in captivity regularly reproduce in their second year. However, yearlings in the wild population reproduce less frquently. During the present study, two yearling females that had conceived were examined, a captive and a free-ranging female. In both cases, the individual was physically advance in development over the average for their age class, with weights 45% and 50% greater than the average. However, in the former case, the probability of survival of the young was greatly reduced, since the parturition was delayed until June. Conception must have occurred some 3 to 4 months after the peak for the wild population.

Puberty in alpacas also seems to be related to physical condition, growth, and development. Novoa *et al.* (1972) found that the average body weight of yearlings that became pregnanat was 40.31 kg as compared to 38.79 kg for those that did not become pregnant, with the difference significant at the P=0.01 level. They related the differences in body weight to the food availability under the study conditions.

7.1.3 Fetal Sex Ratios

Fisher (1930) has shown that under most circumstances, natural selection favors a balanced sex ratio. However, the ability of parents to vary the sex ratio of their offspring in an attempt to maximize their genetic fitness has been proposed by Trivers and Willard (1973). They hypothesized that the relative condition of the female should influence the sex of her offspring, with females tending to produce more males when in excellent condition, and females when in poor condition. Since a deviation from a 50:50 sex ratio would affect all aspects of the dynamics of a population, the possibility of such a deviation must be tested. If the hypothesis of Trivers and Willard (1973) were correct, we would expect a skewed sex ratio in favor of the females, since the females are in relatively poor condition.

The fetal sex ratio information comes from the collection of gravid females, and chulengos hand captured soon after birth. Of the nine fetuses sexed during the present study, only two were males. Females also predominated amoung the hand captured new-born chulengos, with 5 of 7 being female. However, neither sex ratio was significantly different at P=0.05, from a balanced sex ratio (Chi-square of 2.77, with df=1, and 1.28 with df=1, respectively). While these sex ratios are suggestive of differential selection of sex of the offspring by the parents, a larger sample may be needed to make the results significant. If the hypothesis of Trivers and Willard (1973) were correct, we would expect a skewed sex ratio in favor of the females, since in general, the females are in relatively poor condition.

7.1.4 Age-specific Reproductive Rates

The reproductive rate, or fecundity of a population, is defined as the number of live birth per female over a given period of time. Because fecundity changes with age, a description of reproductive performance requires a separate calculation for each age-class. The time interval is usually set at one year for birth-pulse populations, such as most temperate ungulate species.

The current literature on guanaco fecundity is incomlete. Walker (1975) states that the guanaco female breeds every other year, but gives no indication as to the source of the observations. Cabrera and Yepes (1940), Cardozo (1954), England *et al.* (1969a), and others, all indicate yearling breeding. All the above authors agree on a single offspring per year, while Housse (1930) states that up to three young per year is possible, based on observations of an old hunter.

The reproductive rates of the non-migratory guanaco population of the study area were determined by three independent methods: a uterine examination of a sample of females from the population; histological examinations of the ovaries from females collected; and herd composition counts.

7.1.4.1 Collection Data

The reproductive rate of a population could be determined by collecting a representative sample of the females from the population. The limitations of this method are obvious: the individuals must be sacrificed, and it is costly, both for the population and the study, to collect a sufficient number of females.

However, 15 females were collected from the free-ranging population, and throughly examined. The information on the reproductive status of these females is given in Table 14, and the fecundity rates are summarized in Table 15. Since the sample size is small, females over the age of two years have been combined in the latter table. Furthermore, the yearling age class (1 to 2 years old) has been augmented by including two natural, non-starvation mortalities. Even so the reproductive rate

Table 14. The reproductive status, weight, and condition of female guanacos collected on Isla Grande, Chile, 1972-1974.

No.	Age	Date	Weight	LW Ratio*	Pregnant	Lact.	Fetus sex
G2	11.5	8-72	137	1.5	No	Yes	-
G3	0.7	9-72	84	2.0	No	No	-
G4	6.8	11-72	125	1.5	Yes	No	Female
G5	9.8	11-72	117	1.4	Yes	No	Female
G7	6.2	3-73	137	1.4	Yes	No	Male
G10	4.3	4-73	130	1.5	Yes	No	Male
G11	8.5	8-73	-	-	No	Yes	-
I172	3.3	6-74	122	1.5	Yes	No	Male
G15	17.5	7-74	135	1.4	Yes	No	Female
G16	0.5	7-74	78	2.1	NO	No	-
G17	1.5	7-74	120	1.5	Yes	No	Female
G18	7.7	10-74	92	1.9	Yes	No	Female
G19	4.7	10-74	112	1.6	Yes	No	Female
G21	3.8	11-74	104	1.7	No	Yes	-
G22	7.9	12-74	118	1.7	Yes	No	Female
M94	1.8	11-72	-	-	No	No	-
M174	1.6	8-73	-	-	No	No	-

* LW is the condition index, length weight ratio.

Table 15. A summary of the age-specific reproductive rates of guanacos from Isla Grande, Chile, 1972-1974.

Age Class	Sample Size	Number Pregnant	Percent Pregnant
0-1	2	0	0%
1-2	3	1	33%
2+	12	9	75%

of the yearling class is suggestive only, due to the limited sample.

The factors that influenced the sexual maturity of the yearlings, nutrition and physiological condition, also appears to affect the breeding by adults. However, there is little correlation between physical condition during gestation and individual fecundity. Successful conception is most influenced by the condition of the female immediately preceding the breeding season. Hence the preceding winter and reproductive season would be most highly correlated with current reproductive success. This hypothesis is supported by the data from Table 14. Three females that were not pregnant were lactating. In North American elk Cervus canadensis in presumably marginal habitat, Harper (1971) found that cows which had produced and suckled a calf the previous year were less likely to breed than those that had not raised a calf. Conception rates in these two groups were 48% and 75% respectively.

The pattern of fecundity in the guanaco follows that of most mammals, climbing from puberty and leveling off in adulthood. In many animals, notably birds and small mammals, there is a decline in fecundity after middle age. However, this type of declise in slight for large mammals, such as the guanaco. Caughley (1977:84) states that "for the purpose of population analysis, fecundity rate at the plateau can be expressed as a mean value unless curvature is extreme". The importance of the decline in the older age classes is slight because the percentage of old animals is small. The data presented in the preceding Table 15 assumes that there is no appreciable decrease in fecundity in the older age classes.

7.1.4.2 Ovarian Analysis

Since the initial discovery by Cheatum (1949) that estimates of current reproductive rates could be made by examining the ovaries of deer, the method has been applied to several species of ungulates, such as white-tailed deer (Ransom 1967), black-tailed deer (Taber 1953 and Thomas 1970), mule deer (Robinette *et al.* 1955), elk (Morrison 1960), and moose (Simkin 1967).

Examination of the ovarian structures is the only technique that permits the determination of the earlier reproductive histories of individuals. Because scars resulting from corpora lutea of pregnanacy persist in the ovary throughout the lifetime of the female, the entire reproductive history is recorded. Combined with the knowledge of the age of the individual, this information can be used to estimate the long term average fecundity of the population (Thomas 1970).

The use of ovarian analysis depends on several assumptions and conditions. First, there must be evidence that the corpora lutea of pregnanacy (CLP) scars persist throughout the life of the female. Second, the CLP must be distinguishable from other structures, such as the scars from corpora lutea of non-pregnanacy, auxillary corpora lutea, etc. Third, the rate of intrauterine mortality must be known.

The first condition is untested in the guanaco, although females could be aged (see Appendix A) their reproductive histories were not known. If the CLP scars do not persist throughout the lifetime of the individual, the resulting estimate of fecundity would be an underestimate of the true fecundity rate.

However, the latter two assumptions have been discussed in earlier sections, and appear to present little difficulty. Furthermore, the only detailed study of ovarian histology and function in wild ungulates, Thomas (1970), found that the scars from structures other than CLP degenerated rapidly, and could be seen only for one season at most. He also noted that they were readily distinguished from CLP scars.

The ovaries from 13 females from the study were available for analysis. The ages varied from 8 months to 17.5 years, and represented 73 reproductive seasons. Table 16 summarizes the results of the analysis. The number of active CLP and the number of CLP scars is given for each female along with the age of the female. The active CLP are the corpora lutea associated with current pregnanacies, and the CLP scars represent CLP of past pregnancies. It appears from the analysist that the CLP scars do persis for the life of the female, as in deer.

The long term fecundity rate of the guanaco population was determined by regressing the total number of active CLP and CLP scars per individual with the reproductive age of the female at the time of the next parturition. The reproductive age is the number of years of age past the first breeding season, i.e. the actual age

Table 16. The number of active corpora lutea (CL) and corpora lutea of pregnancy (CLP) scars present in the ovaries from guanacos of Isla Grande, Chile.

No.	Age	Active CL	CLP Scars	Total
G16	0.5	0	0	0
G3	0.7	0	0	0
G17	1.5	1	0	1
M94	1.8	0	0	0
G21	3.8	0	2	2
G19	4.7	1	1	2
G7	6.2	1	4	5
G4	6.8	1	3	4
G22	7.9	1	4	5
G11	8.5	0	6	6
G5	9.8	1	4	5
G2	11.5	0	7	7
G15	17.5	1	11	12

minus two years. The regression results are given in Figure 32 and the long term average fecundity of the population is then given by the regression equation. The production of fetuses is described by the equation:

$$Y = 0.366 + 0.762 (X) \qquad (4)$$

where Y is the number of fetuses produced per individual of age X; the intercept, 0.366 is the fecundity of the individuals at first parturition, or at a reproductive age of zero (i.e. actual age of 2); the slope, 0.762 is the

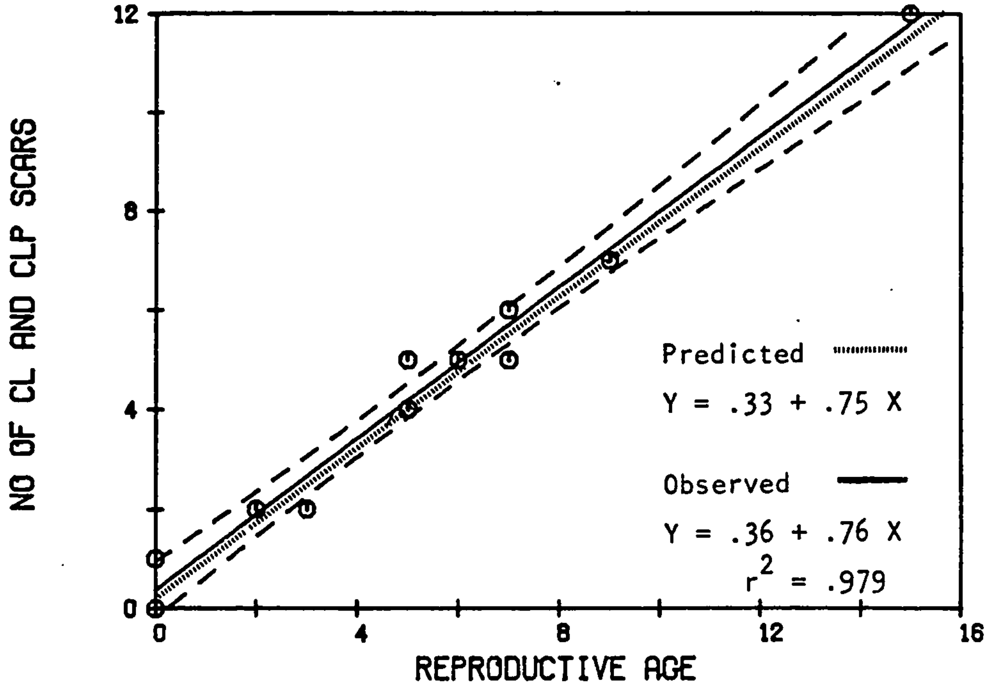

Figure 32. The regression of the number of active CL and CLP scars with age.

fecundity rate of the adults (at a reproductive age greater than zero); and X is the age of the female at the next parturition. The regression is highly significant (P=0.0001), and the R-square is 0.979.

In the preceding section, the assumption was made that there was no decline in the fecundity of the older age classes. This assumption is supported by the regression on CLP scars. If there has been a decline in fecundity with age, the relationship between age and the CLP scars would have been some nonlinear function, with the tail of the line exhibiting a downward curve beyond the prime age-classes of 7 to 8 years. However, the limited data points indicate that a linear function is most appropriate, at least through the 12th year (reproductive age class of 10 years).

7.1.5 Reproductive Rates 1972-1975

The reproductive output of the guanaco population of the study area was monitored by two methods: first, the long term average rates were compared with the pregnanacy rates from the collection data from the study period; and second, by herd composition counts throughout the study period.

7.1.5.1 Long Term Versus Study Period Reproduction Rates

A comparison of the long term average fecundity rates and the pregnancy rates during the study period show no significant differences. The predicted age-specific reproductive rates, based on the collection of a sample of females, summarized in Table 15 is given by the equation:

$$Y = 0.333 + 0.75\ (X) \qquad (5)$$

The observed long term average age-specific fecundity rates, based on the analysis of ovarian structures, was given in equation (4). In the Figure 32, both the observed and predicted (based on equation 3) regression lines are plotted, along with the 95% confidence interval for the observed regression line. The predicted line is contained within the 95% confidence interval, and hence is not statistically different from the observed line at the P=0.05 level.

Unfortunately, the collection sample is too small to allow any comparison between the different years during the study period and the long term average.

7.1.5.2 Herd Composition Data

Herd composition counts are commonly used to determine the fecundity rates of ungulates, since the data are relatively easy to collect and the animals need not be molested. Often it is the only practical means of assessing seasonal and annual changes in reproductive output. However, the interpretation of the data is difficult since the observed young:mother ratios are a function of the age structure of the population, post-natal mortality rates, the survival of the juveniles, as well as the actual fecundity of the adult females.

Herd composition counts were made throughout the year, but counts immediately after the parturition season are the most valuable for the determination of fecundity rates. Table 17 gives the ratios of chulengo:female based on the herd composition counts for the late spring and early summer for the four years of the study. Since the two year-olds can not be distinguished from the older guanacos, the ratios are calculated on the basis of all females over two years of age. Two chulengo:female ratios are given: first, the actual observed ratios, and second, the same ratios that have been corrected for post-natal mortality, using a constant rate for all years. The first line of data, for the month 4/72, was from the first

Table 17. Reproductive rates as determined by herd composition counts for guanacos of Isla Grande, Chile.

DATE	TOTAL GUANACOS	FEMALE GUANACOS	CHULENGO:FEMALE Observed	Adjusted*	95% C.I.
4/72	168	69	.387	.460	±.111
6/72	304	127	.504	.632	±.097
3/73	651	141	.468	.554	±.084
5/73	320	88	.461	.553	±.096
3/74	553	156	.376	.447	±.078
5/74	518	153	.402	.492	±.088
3/75	693	179	.510	.601	±.078

*Adjusted for post-natal mortality

attempt at herd classifications, and the results appear to be an underestimate of the fecundity rates.

The herd composition counts in the table reveal changes in the population reproductive rates over the study period. From 1972 to 1973 the productivity of the herd declined gradually. In 1974 there was a dramatic decline, with a drop from 0.468 to 0.376 young per female. This decline is significant at the P=0.11 level (students t, with z=1.604). The decrease was probably the result of declining productivity accompanying a stable population through mid-1973, and the severe winter of 1973.

From 1974 to 1975 there was an increase in the ratios from 0.376 to 0.510 chulengos per female, significant at the P=0.39 level (z=2.06). This occurred during a period of reduced guanaco and sheep densities on the range, and a mild winter. However, it is impossible to determine if these changes in the young:female ratios were a product of increases in the reproductive rates, or a decrease in the post-natal mortality. It is probable that the mortality of the chulengos would be high after an extremely severe winter such as that of 1973, that must have taxed the gravid females. Therefore, it is most likely that the increase was due to increased chulengo survival.

It should be noted that the reduced ratios for March and May 1974 appear to be underestimates of the real rates, since subsequent counts in December show a ratio of 0.29 (N=221) after most males would have been expelled from the family groups. Hence, the true ratio is probably nearer the upper limit of the confidence interval.

A further consideration in the interpretation of these results is the effect of differential survival of the age-classes from year to year. In ungulates such as the guanaco, where the less productive younger age-classes can not be distinguished from the adults, an increase in the survival of the less productive younger animals can reduce the apparent productivity of the population, even if reproductive rates per adult female have not changed. This appears to have occurred in the 1973-1974 period. After the severe winter of 1973, the yearling females increased from 22 to 28% of the total female population over two years of age. Therefora, without a change in the age-specific fecundity rates, the overall observed productivity dropped from 67% to 62%, since the now more numerous two year-olds are less productive. Hence, a portion of the apparent 1973-1974 decline can be attributed to the change in age structure of the female segment of the population.

Generally, the herd composition data appear to underestimate the actual reproductive rates by 5% or more. On the basis of uterine examination and the analysis of ovaries, the overall reproductive rate should be approximately 65 chulengos:100 females over two years of age. However, in Table 17 the adjusted rates were below this predicted rate. There are several possible reasons for this underestimation: first, the post-natal mortality rates used to adjust the observed ratios could be too low; or second, some of the younger females could have been misclassified as adults. In any case, the ratios must be used with caution.

Two other studies have reported on the reproductive rates in the guanaco, based on herd composition counts. Garrido _et al._ (1977) reported that in Chubut province, Argentina, the rate was 27.4 chulengos per 100 females in March and April. They apparently designated all females, even yearlings, as females. In the present study, the percent of all females over one year of age, with young in March and April was: 35.1% in 1973; 25.5% in 1974; and 41.1% in 1975. Thus it appears that the productivity of the Isla Grande population is greater than that of Chubut. However, the lower reproductive rates reported by Garrido _et al._ (1977) are probably more a function of post-natal mortality rather than any significant difference in fecundity. The chulengos in Chubut are actively pursued for their hides, while in Chile this is illegal.

Franklin (1975) reported much higher productivity for guanacos in Peru. He observed ratios of 34 chulengos per 100 females, and 47 yearlings per 100 adult females, immediately preceding the birth season. The young were then 1 and 2 years of age respectively. These ratios seem quite high. For example, if we assume that in the Peruvian study area the young males were expelled from the family bands, and that the secondary sex ratio was 50:50, then the yearling sex ratio represents either a 94:100 female birth ratio 2 years previous and with little mortality of the young in the 2 year interval, or a lower birth rate with a sharp decline in the relative number of adult females over the same period. If the former is correct, then almost all adults and yearlings had to produce young. It seems more likely that he misclassified some of the females, or that the results represent sampling error due to his small sample size, based on a very short study period of only one week.

7.2 Mortality

In population ecology, the study of mortality includes not only the rate of loss of individuals from the population through death, but also the age-specific mortality rates, life expectancy, generation time, yearly and annual patterns of mortality, causes of mortality, and the difference in mortality patterns between the sexes. Then if possible, we would like to know how these different aspects of mortality are related to population density. Many of these aspects of mortality can be measured directly; however, the study of age-specific mortality, life expectancy, and generation time must be undertaken through the construction of life tables.

The present study of mortality is based on the analysis of guanaco carcasses systematically searched for in the field. A total of 541 carcasses was examined. However, sucn a tally provides a biased reflection of the mortality of the population, since some age classes generally are not properly represented in the tally. Often, the young are underestimated since their carcasses disintegrate rapidly, or are eaten by scavengers and are not found (Taber and Dasmann 1957, Caughley 1966). In the case of the guanaco this seems to have occurred, and hence, the mortality rates of the chulengos will be estimated from the fecundity and population structure data.

7.2.1 Seasonal Patterns of Mortality

A total of 250 guanaco mortalities were calssified as to the season of death. The month of death for chulengos and yearlings could be accurately determined from dentition. The overall seasonal mortality patterns of the non-migratory guanaco population are given in Table 18. The neo-natal mortality was calculated as the difference between the reproductive rates and the observed chulengo:female ratios at the end of summer. The values in the table are the percent of the total annual mortality that occurs in that season of the year, rather than mortality rates for that season. Thus, these values give the seasonality of mortality rather than its magnitude.

Since the migratory population was sampled only on their winter range, no data are available on summer mortality patterns.

Table 18. Seasonal mortality of the guanacos of Isla Grande, Chile in the period from 1972 to 1975

Sex and Age Class	Sample size	Summer	Autumn	Winter	Spring
Female Chulengos	20	47% *	7%	41%	5%
Male Chulengos	17	51% *	6%	39%	4%
Female Yearlings	42	18%	25%	51%	6%
Male Yearlings	29	12%	18%	65%	5%
Female Adults	89	4%	7%	67%	22%
Male Adults	71	6%	4%	63%	27%

* Calculated from the reproductive data and the herd composition counts.

7.2.2 Annual Patterns of Mortality

Mortality patterns are seldom constant over a long period of time. During the study period there was a dramatic fluctuation in mortality which was correlated with changes in the severity of the winter. In the period from 1968 to 1973 the guanaco population recovered from the severe winter of 1968, and had virtually stailized at the 1972 population level (Raul Cassanoca, per. comm.).

However, the winter of 1973 was the most severe on record; snow fell early and persisted throughout the winter. The sheep winter mortality in the Estancia Cameron approached 40,000 head, or about 40% of the total herd, as compared to an average mortality rate of 10%. Guanaco mortality increased from an annual average of 21,3% in 1972 to 44.9% in 1973. In 1974, the year after the die-off, the guanaco mortality was only 9.3%. These mortality rates for the guanaco were calculated from the census data (see Tables 24 and 27).

The changes in mortality in the different age-classes between the sample years were measured by analyzing the age distributions of the mortalities tallied, and testing the differences by a Contingency Table Chi-square test; the differences were considered to be significnat at the P=0.05 level. Four groups were tested: the migratory males; non-migratory males; migratory females; and non-migratory females. The mortality by age class was significantly different between the period previous to 1973 and 1973 for the migratory males (P=0.0134) and the non-migratory females (P=0.0185). In both of these cases, and also in the case of the non-migratory males, the mortality in the severe winter was disproportionately greater in the chulengos and adults over 8 years of age.

the differences in mortality patterns in the non-migratory males and the migratory females were not significant.

7.2.3 Mortality Patterns by Sex

It is common to find differences in mortality patterns between the sexes. These differences are attributed to the physiological drains of pregnancy (Flook 1970), territorial defense (Koford 1957), greater exposure to predation due to social standing (Altmann 1974), differences in the mother-young relations (Taber and Dasmann 1957), and the rigors of rut and reproduction (Geist 1971a, and McCullough 1966).

To test for differences in the age distribution of mortality, the male and female carcass tallies were compared using a Contingency Table Chi-square test for the pre-1973 and 1973 samples.

The differences in the mortality patterns between the sexes were significant in the pre-1973 sample. In general, the males suffered a greater portion of their mortality in the earlier age classes (chulengos through 5 years), and the older age classes (over 10 years of age), while females underwent the heaviest mortality in the middle age-classes. The reasons for these patterns are probably related to the social structure and reproductive patterns. In the early age classes, the young males are without the protection of the family band, and occupy the marginal habitats. For the females, the physiological drain of reproduction takes its toll in the middle age-classes, so these suffer their highest mortality. In the older age classes, the rigors of territorial defense probably increase the relative mortality in males.

However, in the 1973 sample, most mortality was due essentially to winter starvation. There was no significant difference between the mortality patterns of the sexes ($P=0.2448$). The severe winter conditions caused a change in the social patterns of the guanaco which influenced the mortality patterns. Aerial survyes showed that the family bands had abandoned their territories. All social groups were concentrated in the forested areas. Without exclusive access to the better habitats, the females were forced to compete with troop males for the available forage. As a consequence, both sexes exhibited similar age-specific mortality.

7.2.4 Causes of Mortality

For the reconstruction of the dynamics of a population, it is essential to know the factors of mortality acting on the population, and the relative importance of each factor. The importance of these factors will often vary between sexes, age classes, and even years.

The cause of death of the guanacos tallied in the seach for the carcasses are summarized in Table 19. In addition to the overall pattern, three comparisons are

Table 19. The summary of the causes of mortality for guanaco carcasses from Isla Grande, Chile from 1972 to 1975.

	Starvation	Fence	Tree	Hunting	Disease	Misc.	Total N
Total	80.8	6.4	5.0	4.4	2.2	1.0	164
Males	78.8	4.7	7.8	3.6	4.7	0.5	193
Females	82.8	7.3	3.9	3.4	0.9	1.7	233
Pre-1973	84.9	7.4	3.1	2.5	1.9	0.3	324
1973	76.2	5.3	7.9	8.6	0.0	2.0	151
Migratory	88.6	2.1	3.9	3.6	1.2	0.6	332
Non-migratory	65.2	15.2	7.3	6.0	4.3	1.8	164

given: male versus female; pre-1973 versus 1973; and migratory versus non-migratory.

In all cases, starvation is the single most important cause of mortality, accounting for 80.8% of the carcasses classified. These deaths were associated with poor forage conditions in the late winter and early spring. The rates of winter mortality were increased in severe winters. The starvation mortality is particularly high in chulengos and the older age classes. However, the highest mortality for chulengos was still the neo-natal mortality, influenced by the poor condition of the mother, harsh weather, illegal hunting, disease, etc. These losses must be estimated by indirect means.

Accidents make up the second most important cause of mortality, 11.4% of total. The two principal accidents were entanglement in fences (6.4%), and getting feet caught in tree branches when rearing up into the tree to browse (5.0%). Such accidents, like starvation, stem from a shortage of acceptable food and the resulting weakened physical condition.

Illegal hunting was the third most important mortality factor, with 4.4% of the guanacos killed for their hides, for sport, as food for the sheep dogs and pigs, or to elimiate them as possible competitors with the domestic sheep. This figure is undoubtedly low, since the mortality was estimated from the carcass remains in the field, in relation to the total field mortalities. However, many kills were made witnout any field evidence remaining to be found. Also, in the case of the chulengos, their carcasses would disintegrate rapidly, and not be found. Therfore, the chulengo losses due to hunting are not included in the above figure.

Disease appears to play a minor role in control of this population. Sarna or mange (both the sarcoptes and psoroptes varities) was observed in 13.3% of the adult population, but only 2.8% of the adult mortalities could be linked to manage. Generally the susceptibility to this type of disease is symptomatic of poor physical condition. The losses due to mange were only encountered at the end of winter, and animals that did not succumb recovered by early summer.

The only other debilitating disease that was observed was the formation of lesions on the jaw. These lesions may have been caused by at least three diseases: actinomycosis, necrotic stomatitis, and actinobacilosis (Murie 1944). These diseases develop when the tissues of the mouth, especially around the molar teeth, are invaded by fungi through abrasions often caused by eating coarse vegetation. The infected area is either eaten away or enlarged and made spongy. Teeth may be be lost if the area affected is near the toothline. This condition was observed in 3.3% of the adults examined. In general, the disease is not fatal, but there is a reduction in the ability to process and masticate food efficiently. Starvation is more likely to occur in animals affected with this disease.

In many populations, predation is a major cause of mortality. However, on Isla Grande there are no effective guanaco predators, except man. The puma, an important guanaco predator on the mainland (Raedeke 1978) is not present on the island, contrary to the reports of Darwin (1948). The largest predator on the island is the Andean wolf *Dusicyon culpaeus*, which is the size of a large fox or a small coyote. It is now greatly reduced in abundance and distribution due to its supposed predation on the sheep. It is unlikely that it kills many guanacos on the island.

The comparisons in Table 19 demonstrate how mortality factors play different roles in the different segments of the population. Surprisingly, the differences between the sexes were not significant at the P=0.05 level (P=0.0528 with a raw Chi-square of 12.44, with 6 df.). The other two comparisons, between years, and between migrating and non-migrating animals, were highly significant (P=0.001 with raw Chi-square of 22.35 for the comparison between years, and P=0.000001 with a Chi-square of 48.7 for the migrational comparison). It appears that in the severe winter of 1973 the starvation mortality was actually lower than in the earlier years. However, if we combine all the mortality that can be directly linked to the severe winter and the reduced food availability (starvation, trees, and hunting) then we get 90.5% for the previous years, and 92.7 for the severe winter of 1973. With this distribution of causes of mortality, the differences are not significant at the P=0.05 level. Thus the difference between years appears to have been in magnitude and age-distribution of mortality, and not in cause of mortality.

Hunting is included in the winter mortality calculation above since in 1973 the increase in hunting losses resulted from the movement of guanacos into areas heavily used by humans, due to the reduction of available food on the traditional winter range.

The comparison of the migratory and non-migratory guanacos shows that the migratory animals suffer greater starvation losses (winter mortality). In general, the migratory guanacos winter on summer range of the sheep, and most of the preferred forage is removed by the sheep before the arrival of the guanacos. These guanacos then suffer high mortality due to insufficient winter food supply. However, it must be noted that the data are highly biased in favor of winter mortality since the other seasonal ranges of the migratory guanacos were sampled much less intensively.

7.2.5 Life Tables

Life table analysis is a powerful analytical tool that describes the mortality of a population in a manner such that certain characteristics of the population can readily be seen. In life tables, "age-specific mortality rates are presented as if they were progressively depleting a large number of animals born simultaneously. Such a group is called a cohort. Although real cohorts are seldom studied, mortality rates calculated indirectly are applied to imaginary cohorts" (Caughley 1977:85).

The life table consists of five columns: x, the age interval (usually one year in birth pulse populations); dx, the number dying in the year; lx, the number alive at the beginning of each year; qx, the rate of mortality during the year; and ex, the mean length of life remaining for each individual alive at the beginning of the year, commonly called the life expectancy (Deevey 1947). The limitations of life table analysis, and the necessary assumptions of the different methods of life table calculation are reviewed by Caughley (1966 and 1977) and McCullough (1978).

In the present study, the calculation of life tables was based on the age at death from the carcass data. The carcass data were formed into a frequency distribution of deaths in one year intervals, thus forming a "dx" schedule. Subsequent calculations follow that of Deevey (1947) and others. This method is appropriate if the population has a stable age distribution, and if the rate of increase or decrease of the population has been constant for some time, and is known. However, Caughley (1977) states that if the fluctuations in the rate of growth are of shorter periodicity than the time over which the carcasses accumulated, this method will still result in a reasonably accurate life table.

Table 20 gives the life table for the male and females guanacos from the study area, based on the age at death of the guanacos that accumulated over the period from the late 1960's to the summer Of 1973. During this period, the guanaco population appears to have been stable in numbers. The carcasses tallied after the summer of 1973 were not included since the population underwent a drastic change in mortality, thus invalidating this method of life table calculation.

Since the chulengo age class was knowingly underestimated by the carcass tally, the "lo" frequency was estimated from the fecundity rates by the formula:

$$lo = \sum lx \; mx \qquad (6)$$

where "mx" is the mean number of female offspring produced per female age "x" years. The "do" frequency is then "lo" minus "l1".

From the values in the life table, we can readily assess the patterns of mortality with regards to age. For both males and females, the mortality can be divided into two phases - a juvenile phase, characterized by moderately high rates of mortality, followed by an adult phase in which the rate of mortality is initially low, but rises gradually until the age of 9 years. The variability in

Table 20. A life table for the non-migratory guanaco population previous to the winter of 1973, for the intensive study area, Isla Grande, Chile.

MALES					FEMALES				
x	dx	klx	qx	ex	x	dx	klx	qx	ex
0	70	1000	.313	4.49	0	61	1000	.272	4.39
1	28	687	.182	5.30	1	29	728	.178	4.85
2	13	562	.103	5.37	2	15	598	.112	4.79
3	13	504	.115	4.93	3	14	531	.118	4.33
4	8	446	.080	4.51	4	12	469	.114	3.84
5	12	411	.130	3.86	5	12	415	.129	3.27
6	14	357	.175	3.36	6	17	362	.210	2.68
7	17	295	.258	2.97	7	27	268	.422	2.67
8	14	219	.286	2.83	8	20	165	.541	2.55
9	12	156	.343	2.75	9	4	76	.235	3.97
10	7	103	.304	2.94	10	2	58	.154	4.04
11	4	71	.250	3.00	11	1	49	.091	3.68
12	2	54	.167	2.83	12	1	45	.100	3.00
13	3	45	.300	2.30	13	3	40	.333	2.28
14	2	31	.286	2.07	14	2	27	.333	2.17
15	2	22	.400	1.70	15	1	18	.250	2.00
16	1	13	.333	1.50	16	1	13	.333	1.50
17	1	9	.500	1.00	17	1	9	.500	1.00
18	1	4	1.000	0.50	18	1	4	1.00	0.50

rates in the older age classes (over 9 years) is probably due to sampling error, as the sample frequencies were quite small. This overall pattern is similar to that of most mammals studied to date, and especially for ungulates (Caughley 1966).

While the general pattern is similar for both sexes, there are differences both by age distribution of the mortality, and in magnitude. Figure 33 plots the survivorship curves for both males and females, based on the "Lx" column. The vertical axis is logarithmic, since if mortality were constant in all ages, the result would be a linear relationship between age and survival on a plot such as in the figure. The figure shows that the males suffer slightly higher mortality in the age classes from 0 to 6 years, while the females suffer higher mortality from 7 years on. Overall, the males have a higher survival rate, as indicated by the higher average life expectancy at birth (4.49 versus 4.39). The result is a slightly skewed sex ratio in the simulated life table population as a whole (4989 males versus 4875 female if we start with an imaginary population with 1000 individuals of each sex at age zero). Excluding the chulengos, the male:females adult sex ratio was 105:100.

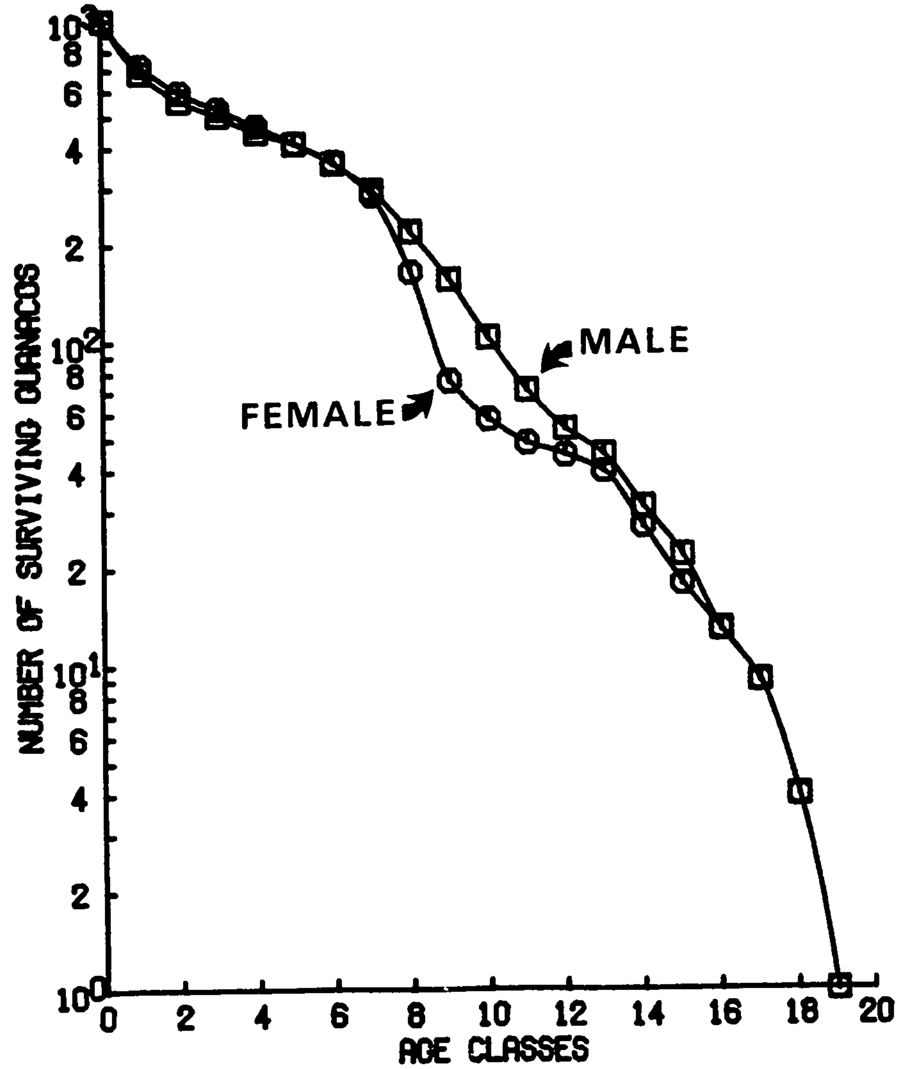

Figure 33. The survivorship curve for both male and female guanaco populations on the intensive study area. The curves are based on the life table presented earlier.

7.3 Movements

A local population can gain or lose members not only through natality and mortality, but also through immigration and emigration. Studies have shown that both sorts of movement can be important factors in the annual dynamics of mammalian populations. Myers and Krebs (1971) and Gentry (1968), working with small mammal populations, both documented emigration of juveniles and subordinate individuals, and postulated that this was a principal mechanism of population regulation. Taber and Dasmann (1958) found an emigration rate of 35% for yearling female black-tailed deer, while the males were reduced by hunting.

Fragmentary and circumstantial evidence indicates that the movement of guanacos between the population of the study area and the rest of the island is an insignificant factor in the annual cycle of population dynamics.

Since the study area population is bordered by the inhospitable Andes mountains on the south, and the oceans on the east and west, the only area for movement is to the north. The guanaco population in the area to the north could not serve as a source of any significant number of immigrating guanacos since the area supports very few guanacos, and the scattered populations that do persist appear to be stable in numbers. All newborn are recruited into the local populations. These populations appear to fluctuate in the same manner as the main population of the study area.

The loss of individual guanacos through emigration is considered to be insignificant for two reasons. First, the observed changes in population structure and abundance can be almost fully accounted for by natural mortality within the study area. Second, social pressures which generally cause emigration or dispersal in mammals (Wilson 1975, Caughley 1977, and Barash 1977) from the best habitat to less favorable habitat, could not be expected to operate for a population such as the guanaco of Isla Grande that are at reduced densities on the primary range. Locally, territorial males do expel juvenile males from the band and displace male troops. However, these males have little trouble occupying suitable habitat between the territories of the family bands, within the general range of the population, and there would be little advantage gained by a family band that would force other individuals from the area outside of their own territory. Without such pressure, it is unlikely that any significant amount of movement to inferior habitat would occur.

7.4 Population Structure

A knowledge of the sex and age structure of a population, in addition to mortality, natality, and movement is necessary for the study of the dynamics of a population (Eberhardt 1969). Further, as we have seen in earlier sections, an understanding of the changes in population structure over time can be used to infer annual variations in recruitment, age-specific reproductive rates, and relative mortality rates, which can not be measured directly.

7.4.1 Herd Composition Counts

The sex and age structure of the guanaco population of the study area was determined through herd composition counts throughout the study period. The results of these counts are summarized in Table 21. All values are expressed as a ratio to 100 adult females (two years old and older). Originally, the guanacos were classified into the five catagories listed in Table 2. However, it was nearly impossible to separate the different age classes in the male troops, so the males above one year old were combined into a single age class. Therefore, four classes

Table 21. A summary of the herd composition counts from the Isla Grande study area, 1972-1975.

Date	Sample size	Males	Adult Females	Yearling Females	Chulengos
4/1972	168	69.5	100	22.1	38.7
6/1972	304	113.3	100	-	50.4
8/1972	110	203.4	100	13.8	62.1
9/1972	102	92.8	100	7.1	42.8
11/1972	122	103.8	100	3.8	26.9
1/1973	239	120.9	100	12.8	44.2*
3/1973	651	189.7	100	16.7	46.8
4/1973	275	91.7	100	21.1	44.4
5/1973	320	110.2	100	15.6	46.1
8/1973	104	121.6	100	21.6	37.0
9/1973	156	139.3	100	12.6	25.0
10/1973	236	124.1	100	16.1	29.8
12/1973	345	166.9	100	16.0	25.0
3/1974	553	127.8	100	22.4	37.6
5/1974	518	128.9	100	15.2	40.2
6/1974	184	108.1	100	12.4	35.1
9/1974	351	140.8	100	22.5	29.2
10/1974	478	136.7	100	13.8	37.3
11/1974	165	125.4	100	14.3	36.3
12/1974	1882	158.4	100	10.0	26.3
1/1975	697	87.1	100	27.8	38.8*
3/1975	693	186.1	100	24.6	51.0

*Parturition is not yet completed at this time.

were used: adult males, adult females, yearling females, and young of the year.

In the first year of study, inexperience with the identification of the different age classes in the family groups caused an apparent underestimation of the number of yearlings present. Consequently, the low percentages of yearlings in 1972 and early 1973 samples probably do not represent low recruitment rates, but rather sampling error.

The difficulty of assessing population structure by means of herd composition is shown in Figure 34, and Table 21. Since the guanaco forms social groups of highly variable size, large samples are necessary to overcome sampling error due to aggregation. To demonstrate the possible sampling error, a large sample of 550 individual classifications was divided into interpenetrating subsamples of different size. The average deviation of the subsamples from the mean of the large sample was calculated for each subsample size, and plotted in Figure 34. On the basis of this data, it would be necessary to classify at least 200 individuals to estimate the young:female ratios within 5% of the large sample results. This is considerably greater than the variability expected in animals that fit a normal distribution, that is, that

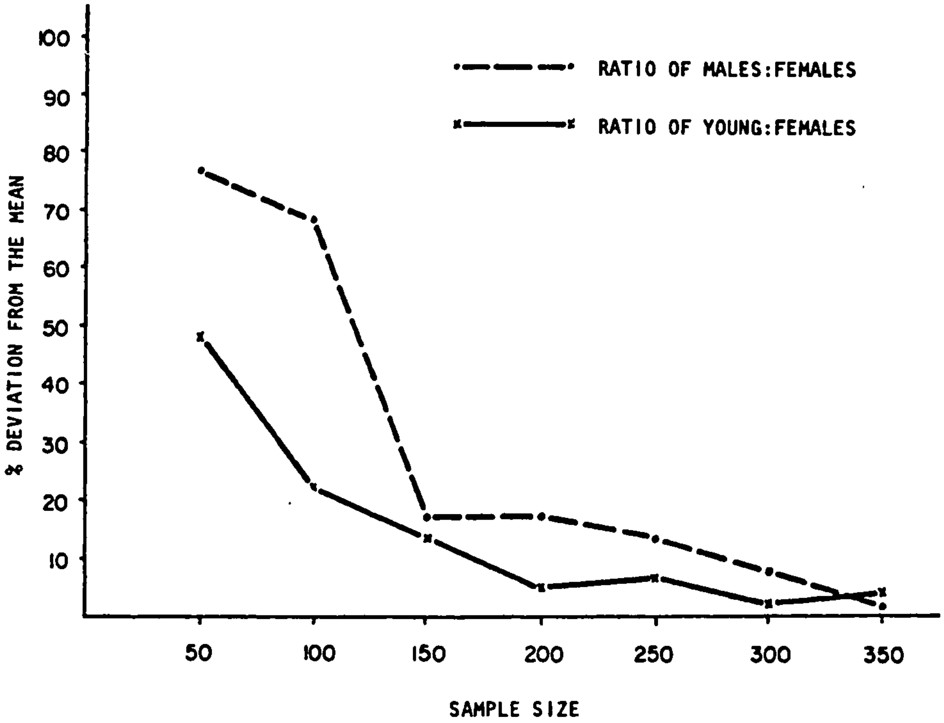

Figure 34. Deviations of herd composition count means from the mean of a large (500) sample size.

are not aggregated.

Large sample size alone will not solve the problems of interpreting herd composition data. For example, in Table 21 we see a great difference in the male:female ratios in December 1974, January 1975 and March 1975, even though the samples were quite large. It is unlikely that half of the male population died during the period, and then the following month the females died, thus balancing the sex ratios. The differences are more likely due to sampling error. Hence the best data would be from large sample sizes throughout the year that could be averaged or regressed over time. Samples taken only once or twice a year may be misleading unless the sample is taken at the right time, and all sex and age-classes are properly represented in the sample.

7.4.2 Adult Sex Ratios

The herd composition counts indicate a skewed sex ratio favoring the males. The average ratio of males to females (excluding the chulengo age class) was 112:100, which is significantly skewed (raw Chi-square of 54.5, with df=21) at the P=0.05 level. This would indicate a higher survival rate for the males, since there is no evidence of a skewed sex ratio at birth favoring the males.

These results show a higher proportion of males in the population than was observed in the analysis of age structure based on the life tables. The later data indicated a sex ratio of male:females (excluding chulengos) of 105:100. However, the differences between these two estimates of sex ratio are not significant at the P=0.05 level (raw Chi-square of 0.1079 with df=1).

The sex ratios of adults do not appear to have changed over the study period. The yearly average ratio of males to 100 females were: 109.4 in 1972, 113.6 in 1973, 112.1 in 1974, and 109.3 in 1975.

7.4.3 Age Structure

A detailed description of the age structure of a population is seldom possible through field observations, since most age classes are not visually distinguishable.

The population often can only be divided into broad categories such as young, yearlings and adults. This type of data has been presented for the guanacos in Table 21. A more detailed analysis of age structure was presented an earlier section based on life tables.

The post-parturition age structure of the female segment of the population is presented in Table 22. The values in the table were derived by averaging the various sample values in Table 21. The tabled values for the 2-3 year-olds are the average number of yearlings present in the pre-parturition population, since it is assumed that no mortality occurs from 12 to 24 months of age. In general, the 2-3 year-olds appear to be underestimated in

Table 22. The age structure of the female segment of the guanaco population of southern Isla Grande, 1972-1975.

Year	Adult females	2-3 Year-olds	Yearlings	Chulengos*
1972	100	-	17.9	50.4
1973	100	10.5	17.6	45.8
1974	100	14.9	18.1	37.3
1975	100	12.7	26.2	51.0

*Chulengos includes both males and females

the table, which would indicate that the number (survival) of the 1-2 class was underestimated.

A similar analysis of the male population is not possible since yearling males could not be consistently distinguished from the adults.

7.5 Population Size

The estimation of the number of wild animals in a population is notoriously difficult, and consequently the problem has received considerable attention. Seber (1973) gives a recent review of the general subject.

The guanaco population size of the intensive study are was estimated using line transect methods. A census of the entire area was conducted in the months of October and November in 1972, 1973, 1974, and December 1977. Since by this time the majority of the migratory guanacos had departed their winter ranges within the study area, the estimates are of the non-migratory population only.

The total population size "N" was calculated from the line transect data by three methods, based on different theoretical functions for the probability of sighting an animal at a given distance from the transect. This function is formally referred to as the sighting probability function, written as g(y). These three methods are the Gates method, the strip census, and the non-parametric line transect method. All three methods make the assumption that the animals are distributed randomly within the census area "A". The population estimators and the theoretical variances used in the study are given in Table 23.

The Gates method (Gates *et al.* 1968) is based on the assumption that the function g(y) is a negative exponential. With this model, the probability of sighting an individual animal decreases exponentially with an increase in the distance from the transect. A further

Table 23. Estimators of population size, and theoretical variances used in this study.

Estimator	Population estimation $\hat{N}$	Theoretical variance estimate of $\hat{N}$
Gates	$\frac{An\ (n-1)}{2L\ \Sigma Y_i}$	$\frac{n}{p^2}\ (1-p+\frac{n}{n-2})$
Strip	$\frac{P(0,W)}{2LW}$	$\frac{n}{p^2}\ (1-p)$
Non-parametric	$\frac{1}{2}\left[\frac{3P(0,\Delta)-P(\Delta,2\Delta)}{\Delta}\right]\frac{A}{2L}$	$\frac{A\hat{N}}{2L}\ (2.5/\Delta)$

Legend: P(a,b) = frequency of animals in the distance between a and b

$$p = \frac{n}{\hat{N}}$$

assumption is that the probability of sighting an animal on the transect is one, i.e. $g(0)=1$. The theoretical variance of the estimator is given by Quinn (1977).

The strip census estimator is the simplest non-parametric estimator, and is based on the assumption that all animals within a distance d of the transect are seen, that is, $g(0,W)=1$. The method is quite simple since all one needs to determine is whether or not an animal is within the strip of predetermined width W. The variance of the estimator is from Quinn (1977).

The non-parametric method has been described by Seber (1973), Quinn (1977) and Eberhardt (1978). This method makes no assumption about the sighting probability function. It is based on the proportions of observations falling in two arbitary, equal sized intervals out from the transect, designated as P(0,D), and P(D,2D), where D (usually represented as the greek letter delta) is the width of the interval. "The choice of the delta depends on a compromise between bias due to the approximate nature of the equation, and the need to use a substantial fraction of the observations" (Chapman et al. 1977:32). Eberhardt (1978) suggested that from 66% to 75% of the observations might be included with 2 delta of the transect line for a bias of roughly 10%. The theoretical variance estimator is from Quinn (1977).

The results from the different census years, and analytical treatments is given in Table 24. The population estimators with the corresponding 95% confidence intervals are given for the different methods. There is general agreement between the different population estimators within all years, except the 1977 census, which was not conducted by the author. For 1972, there is no statistically significant difference between the different estimators at P=0.05. In all cases, except where the variance was calculated by the interpenetrating

Table 24. Population size estimates for the non-migratory guanacos of the intensive study area of Isla Grande, Chile.

Method	YEARS			
	1972	1973	1974	1977
Gates	5373 ± 746	3758 ± 507	4294 ± 503	5371 ± 196
Gates[1]	5373 ± 1674	-	-	5371 ± 2244
Strip	4671 ± 1136	-	-	1956 ± 489
Non-parametric[2]	5616 ± 456	-	-	-
Non-parametric[3]	6319 ± 808	-	-	-
Non-parametric[4]	-	-	-	5730 ± 598

Notes:

1. Variance estimate based on interpenetrating sample method of Seber (1973)
2. The Δ was set at 0.15 kilometer.
3. The Δ was set at 0.20 kilometer.
4. the Δ was set at 0.30 kilometer.

sample method of Seber (1973) the variance estimates must be considered a minimum variance estimates due to the violation of the assumption of random (i.e. non-aggregated) distribution of the guanacos on the range (Quinn 1977). The further ramifications of the violation of this assumption will be considered below.

Since guanacos are distributed in aggregated social groups, the assumption of random distribution seems to be violated. Quinn (1977) conducted computer simulation studies to determine the effects of aggregation on the line transect estimators. He found that no bias is induced in the abundance estimates by the increase in aggregation. His studies showed that the choice of the sighting probability function g(y) was the most important factor in determining the bias of the estimates of population size. He concluded that parametric methods such as the Gates model should be used only when the goodness-of-fit test does not reject a chosen sighting probability model, and that non-parametric estimators should be calculated for comparison.

The appropriatness of the Gates model was tested by a Chi-square test of the observed and predicted distributions of the guanaco sightings with regard to distance from the transect. Table 25 gives the number of

Table 25. A comparison of the observed and predicted guanaco distributions in relation to the transect. The predicted distribution is based on the negative exponential model.

Right Angle Distance in Meters	Number observed	Number predicted*
0- 50	64	64
51-100	57	57
101-150	47	51
151-200	37	45
201-250	55	40
251-300	42	36
301-350	20	32
351-400	30	28
401-450	31	25

*Based on the negative exponetial model of:

$$N = e^{-2.3287(X)}$$

guanacos observed, and the predicted number on the basis of the negative exponential model, for the different distances from the transect. A comparison of the two distributions gives a Chi-square value of 14.78, with 9 degrees of freedom, which is not significant at the P=0.05 level. On the basis of this test, I would conclude that there is no lack of goodness of fit, and that the Gates model is appropriate for the analysis of the line transect data.

The second assumption, that all the guanacos on the transect are observed (i.e. $g(0)=1$) must also be evaluated. If this assumption is violated, the estimator would underestimate the population size (Eberhardt 1978). However, for ground based censusing in generally open habitat, the probability of sighting a guanaco within even 50 meters of the transect must be close to unity. The social organization of the guanaco, its diurnal habits, and large size all contribute to make the guanaco highly visible along the transect lines.

7.6 Reconstruction of Population Dynamics

The purpose of the study of population dynamics of any species is to assess the present status and probable future trends of the population, and to evaluate what the population characteristics reveal about the factors limiting the population growth. The raw data of the dynamics of the guanaco population have been presented in the preceding sections, and will now be used to model the dynamics of the population during a typical year at equilibrium population size, and then to reconstruct the dynamics of the population over the entire study period. From these models we can then evaluate the response of the population to its environment, and to the annual fluctuations in the carrying capacity caused by the environmental changes.

7.6.1 The Annual Cycle

In the period preceding the winter of 1973 the guanaco population appeared to be stable in numbers. Sheep and guanaco mortality had not changed over the period since about 1968, and weather conditions were reported to be about normal (Raul Cassanova, per. comm.). Furthermore, the first census in April 1972 gave a population estimate of 7047 (with a 95% confidence interval of 5986 to 8108), which is not significantly different from the April 1973 estimate of 6520 (with a 95% confidence interval of 5835 to 7205).

In Table 26 the changes in population numbers and structure that occurred through this "typical" year at population equilibrium are reconstructed, based on all available data. The table begins with the post-partum population, before the neo-natal mortality, and follows the decline in population numbers through the entire year. The dynamics of this population are characterized by a high rate of neo-natal mortality in both sexes in the first months of life (15% for females and 18% for the

Table 26. Dynamics of the guanaco population of the study area, Isla Grande, 1972.

	Jan 15	Summer losses	Apr 15	Fall losses	July 15	Winter losses	Sept 15	Spring losses	Dec 15	Jan 15
Females										
Chulengos	724	114	610	15	595	97	498	8	490	724
Yearlings	490	16	474	22	452	44	408	5	403	490
Adults	2199	17	2182	28	2154	269	1885	88	1797	2199
Total	3413	147	3266	65	3201	410	2791	101	2690	3413
Males										
Chulengos	724	131	593	16	577	103	474	12	462	724
Yearlings	462	10	452	15	437	54	383	4	379	462
Adults	2221	22	2199	15	2184	254	1930	88	1842	2221
Total	3407	163	3244	46	3198	411	2787	104	2683	3407
TOTAL	6820	310	6510	111	6399	821	5578	205	5373	6820

males), nearly balanced sex ratios throughout the year, similar mortality patterns for males and females, and a high winter mortality rate. This winter mortality, associated with the reduction in forage quality and availability, removed approximately 16% of the summer population, and accounted for 70% of the total mortality. Winter mortality was the only important mortality agent for the adults.

7.6.2 The Population Dynamics 1972-1975

With the exception of the first season, 1973, the guanaco population of the study area changed in size and composition each year. These changes were monitored through the annual censuses given in Table 24, and the herd composition counts. Table 27 follows the non-migratory guanaco population through the entire study period, starting with the post-partum population in 1972. The November population estimates come from the census data, while the January estimates are calculated from the mortality and natality data.

The changes in population size from year to year were related to the availability of suitable seasonal forage. From the late 1960's through the summer of 1973 there was

Table 27. Dynamics of the non-migratory guanaco population of the study area, over the entire study period, from 1972 to 1975.

	Jan. 1972	Nov. 1972	Jan. 1973	Nov. 1973	Jan. 1974	Nov. 1974	Jan. 1975
FEMALES							
Chulengos	724	490	724	399	488	442	552
Yearlings	490	403	490	311	399	326	442
Adults	2199	1797	2199	1198	1509	1362	1688
Total	3413	2690	3413	1908	2396	2130	2682
MALES							
Chulengos	724	462	724	379	488	441	552
Yearlings	462	378	462	284	379	354	441
Adults	2221	1843	2221	1187	1471	1369	1723
Total	3407	2683	3407	1847	2338	2164	2716
TOTAL	6820	5373	6820	3758	4734	4294	5398

little annual variation in winter weather patterns, and the guanaco numbers were relatively constant over the period. However, the sheep population increased over this same period as a result of expropriations, new management goals and politics (Raul Cassanova, per. comm., and Garcia 1969). The mortality of both sheep and guanacos in the winter of 1973 was caused by range depletion combined with an early, persistent, heavy snowfall. Guanacos and sheep were restricted by snow to the forest zone where there was less snow on the ground due to crown interception. In the forest, the only food for them was the browse from trees and shrubs. The guanaco population declined to a low of 3758 in November 1973. After the severe winter of 1973, the guanaco population began a gradual recovery in numbers. The guanacos reached a population of 5371 in 1977, which equals the 1972 population size. The population was still increasing in 1978 (see Table 24), presumably in response to moderate winters.

7.6.3 Carrying Capacity

From the data presented above, it is possible to estimate the mean carrying capacity of the guanaco range in the study area. For any population with density dependent population dynamics, carrying capacity is the the population size where the average rate of increase is zero, for the existing conditions.

To determine if the population was responding to its environment in a density-dependent manner, and to estimate the carrying capacity for the herd, the rate of population change was regressed on population size (Figure 36). The data in the figure come from the census data collected during the study period, and the 1977 census. The regression is significant at P=0.01, with an R-square of 0.613, and the relationship between population size and growth is negative, as expected if the population were responding in a density-dependent manner. With an increase in population size, the rate of population growth decreases or becomes negative. The estimated carrying capacity is approximately 5200 guanacos. Furthermore, if the regression is truly linear, then the maximum rate of growth is at K/2, or approximately 2600 guanacos (McCullough 1978). At this point, the growth rate is 28%

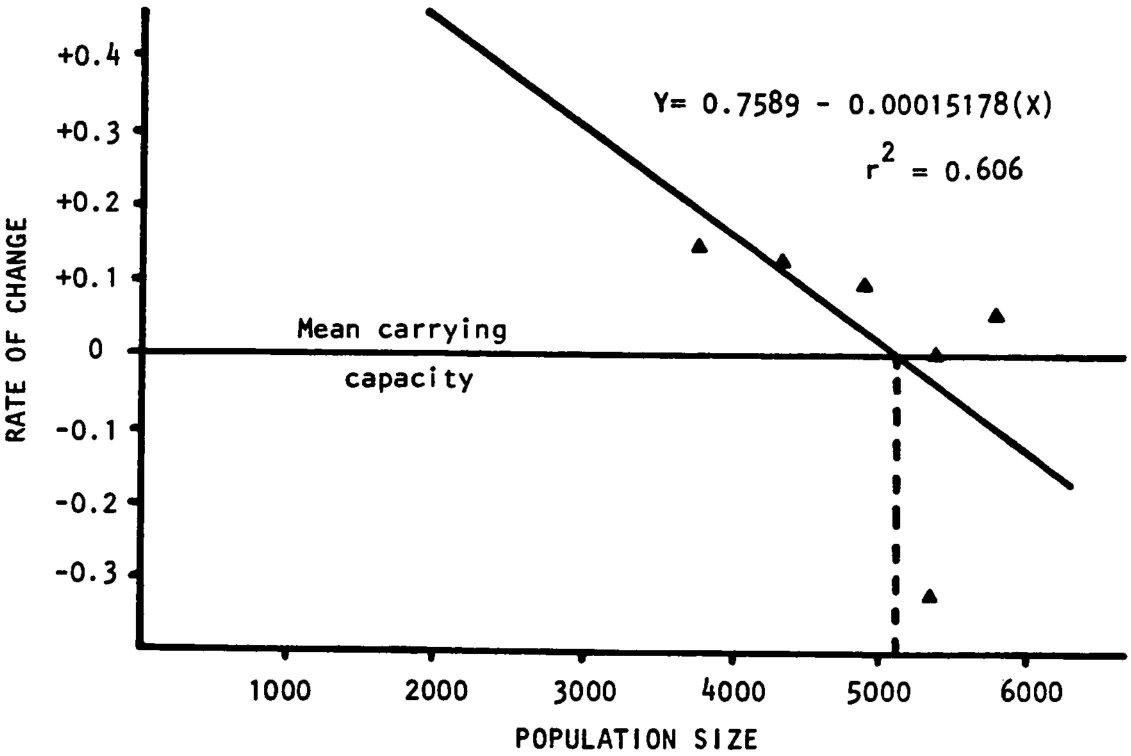

Figure 35. The regression of the rate of population change on population size for the guanaco population of the intensive study area, 1972-1977.

annually, or an increment of 728 individuals; this is the point of maximum herd productivity.

This model assumes a constant environment. Since the winter of 1973, the sheep population has been reduced by harvesting, in an attempt to help the range recover from past overgrazing. Hence, if we consider only the post-1973 data, then the estimated carrying capacity of the range is approximately 6500. Conversely, any changes in the management of the sheep, such as the division of the range into smaller, more havily stocked, ranches could adversely affect the carrying capacity for the guanaco.

7.6.4 Assessment of Population Growth Characteristics

In the guanaco population, the variable parameter limiting population growth is survival rates. In the period of population expansion, after the winter of 1973, the reproductive rates were at best equal to the rates in the period before 1973, when the population was stable. In Table 17 the young:female ratios showed an inital decline in the reproductive season following the severe winter, reflecting the poor condition of the females. By 1975 the reproductive rates had recovered to the pre-1973 levels. However, even while the population continued to expand, the reproductive rates were held at the pre-1973 levels. In December 1977 the young:female ratio was 29.6:100, and the yearling female:adult female ratio was 14.8:100 (C. Cunazza, unpublished data). These ratios are comparable to the 1972 and 1975 levels. Thus it appears that the guanaco, unlike the North American deer and elk, do not respond to lowered population density with an increase in reproductive rates, but rather by a reduction in the mortality rates of the adults and yearlings. This result in guanacos is similar to that of caribou as described by Bergerud (1971) in Newfoundland.

The cycle of population dynamics of the guanaco follows the pattern that is typical of many temperate ungulate populations. After the initial period of establishment in an environment, they tend to fluctuate around some mean population size (Riney 1964, Caughley 1970 and 1977). In some populations these fluctuations are quite dramatic (McCullough 1966), while in others the oscillations are damped. Several mechanisms causing these fluctuations have been proposed. Caughley (1977) has developed a model of these types of fluctuations based on an interaction of the herbivores and their forage resource, similar to the classical predatory-prey models. The model is a variation of a density-dependency of the herbivore on the resources of the habitat. Andrewartha and Birch (1954) have proposed that these fluctuations in population numbers are density-independent responses to changes in the physical environment, such as weather. Others have proposed fluctuations in the forage resource that cause a change in the carrying capacity of the environment.

The changes in the guanaco population numbers over time are a density-dependent response to changes in the carrying capacity of the range. The carrying capacity of the range is in turn at its lowest in the winter, and population dynamics are most affected by the forage availability in the winter months. An important short term factor that reduces the winter carrying capacity is the severity of the winter weather. However, unlike the model proposed by Andrewartha and Birch (1957), the guanaco population will stabilize even with periodic severe winters. The severity of the winter weather rather than being the ultimate factor in population regulation is a proximate factor, causing a fluctuation or variance in population around the mean carrying capacity.

CHAPTER 8

Population Dynamics of Domestic Sheep of Magallanes

The evaluation of competition between two species starts with a model of the growth processes of the two populations, and an analysis of the factors that appear to limit the population growth. In this chapter, the population dynamics of the domestic sheep that share the range with the guanacos will be examined from the introduction of the sheep until the present. This information will be used in the models and analysis of competition in the next chapter.

The analysis of sheep population dynamics is based on the records of the "Sociedad Ganadera del Tierra del Fuego", since its founding in 1894. This sheep ranching company was the largest in the province and at one time controlled over 3,000,000 hectares of the best ranching land and best guanaco habitat. At its peak in 1934, the sheep herd of the company totaled 1,354,283 animals. This company controlled the Estancia Cameron until it was expropriated in 1970.

The records of the company that are available include data on: the total sheep population, annual mortality rates, the number of reproductive females, the number of lambs produced that survive to the "marking" stage, the annual wool production, and the number of sheep harvested. In all cases, the data are actual counts, not estimates.

8.1 Population Growth

The growth of the sheep herd of the Ganadera is given in Figure 36. Since the total number of hectares in the ranching system has varied over the period, the sheep numbers have been converted to density (sheep per hectare) in the figure.

Four distinct growth stages are represented in the graph: rapid expansion of the herd from 1894 to 1934, gradual decline from 1935 to 1955, renewed expansion from 1955 to 1966, and rapid growth from 1966 to 1970.

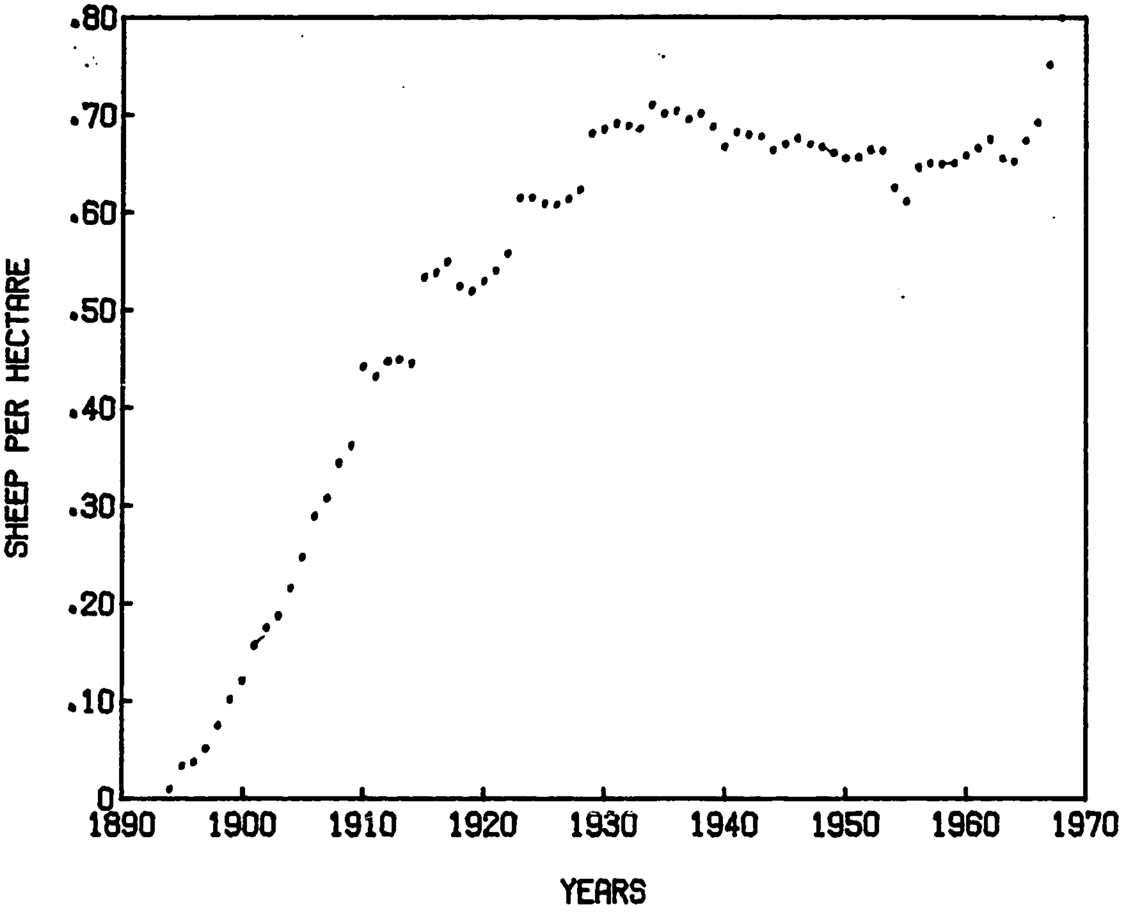

Figure 36. Growth of the sheep population of the Ganadera since introduction in 1894. The sheep population size has been converted to sheep densities.

During the expansion period from 1894 to 1925 the sheep densities on the Ganadera lands increased in a super logistic manner. The increase in density was accelerated by purchases of sheep, and the concentration of stock following expropriation of lands in 1914, 1922, and 1928. Both the population density, and the total sheep numbers peaked in 1934, whith sheep densities reaching 0.74 sheep per hectare. The inflection point in the curve of population growth occured in 1909 at a density of 0.37 sheep per hectare. In logistic growth models, the inflection point occurs ar K/2, which in this case corresponds exactly to the observed inflection value.

Apparently, the peak in densities in 1934 represented a slight overshoot of the carrying capacity of the range, since the densities declined after 1935. This decline in sheep densities does not appear to have been a management decision. As we shall see in a later section, the annual harvest rates were actually reduced over this period, in an apparent attempt to maintain high sheep densities. Rather, the reduction in the sheep densities appears to have been due to a reduction in the carrying capacity of the range due to overgrazing (Erasmo 1972). By 1955, the density had declined to 0.62 sheep per hectare, a decrease of 12% in 20 years. Corroborative evidence, supporting the hypothesis of an overshoot of K, and subsequent range deteriortion, is the decline in wool production from 2.86 kg/ha to 2.54 kg/ha in the same period.

In 1955 the Ganadera began a major program to improve the range through the removal of the shrubs that had increased with overgrazing. From 1955 to 1966, over 73,000 hectares of shrublands were mechanically cleared and seeded with introduced grasses (Erasmo 1972). These range land improvements increased the carrying capacity of the range, and sheep densities increased from 0.65 to 0.69 sheep per hectare, without a reduction in harvest (see Figure 37 for the harvest rates).

Further land expropriations began in 1966. The range improvements were discontinued. In the first expropriations in 1966 and 1967 only the land was expropriated, and the company was free to move their sheep herds to their remaining holdings, thus greatly increasing the short term densities. The final expropriations occurred in 1970, and completely eliminated the Ganadera as a management unit. The new smaller sheep ranches, such as the now communally managed Centro de Producion Cameron attempted to maintain these excessively high sheep density, and disastrous losses occurred in the first harsh winter, in 1973. The post-1973 sheep density was been reduced from 0.86 to about 0.72 sheep per hectare, which approximates the original K.

8.2 Sheep Reproduction

The principal cause of increase in the sheep population has been reproduction, since introductions were numerically important only in the initial years after establishment of the farms. The reproductive output of the sheep population is dependent on two factors: the reproductive rates of the ewes, and the relative number of reproductive ewes in the population. This latter factor is especially important in domestic herds since the sex ratios in the population are directly influenced by management.

In Figure 37 the productivity of the ewes in the population, measured as the number of lambs per ewe at the time of weaning, is plotted over time. The lambs are weaned at about 45 days of age, hence the reproductive rates are actually affected by lamb survival, and could be considered to be lamb recruitment to age 45 days. There is a distinct trend of increase in reproductive rates from 1894 to 1928. This trend is most likely due to improved range management, including a reduction in predation loss to the natural predators and the remnants of the Ona Indians, fencing of pastures, and more intensive animal management.

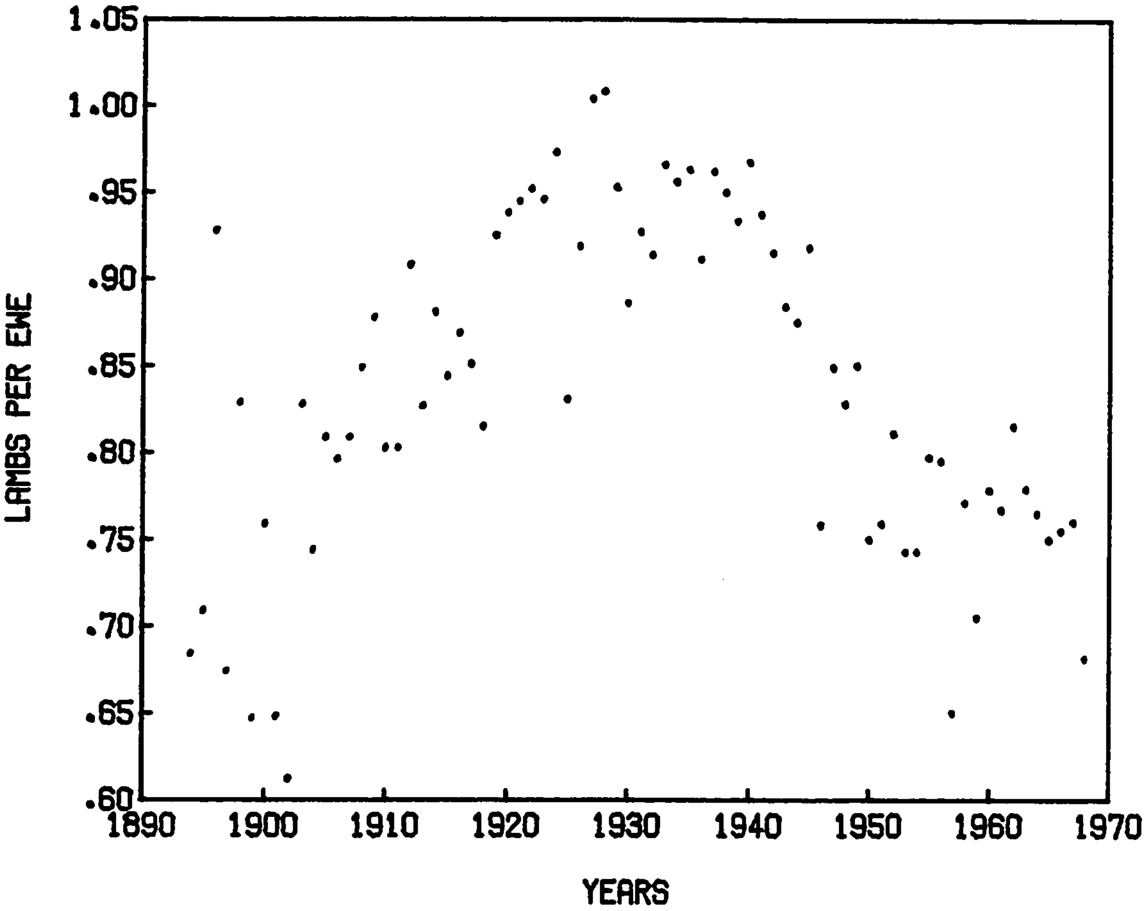

Figure 37. Lamb productivity of the ewes of the Ganadera over time.

The reproductive rates of the ewes peaked in 1928, six months before the peak in sheep density. The rates have declined to the present, following a linear pattern, described by the regression formula:

$$R=0.927 - 0.0076(T) \qquad (7)$$

where R is the number of lambs per ewe, and T is the number of years since 1928, when the rates peaked. The regression is significnat at the P=0.00001 level, with an R-square of 0.76.

In an earlier paper (Raedeke 1978) I hypothesized that the decline in lamb productivity of the ewes was due to the generally accepted, but poorly documented, decline in range condition of the region. For example, Correa (1972) found a high rate of embryonic mortality and a low ovulation rate in the Correidale ewes of Isla Grande. He suggested that the resultant low reproductive rates may have resulted from the "poor feeding" conditions. However, it has also be suggested that this decline in lamb productivity was due to a gradual change in the breeding stock from Romney Marsh sheep to Correidale (E. Tafra and D. Newing, per. comm.), starting in the 1920's. They argued that the Romney Marsh are more prolific than the Correidale which were imported because of their higher production of wool and meat. While this change in breeding stock is undoubtedly a contributing factor, the difference in reproductive rates of the two breeds is not sufficient alone to account for the 36% decline in lamb production in a 40 year period (Kammlade 1947, and Harmsworth and Page-Sharp 1970). Further, the correspondence of the time of decline in the lamb production and the population as a whole reaching carrying capacity supports the hypothesis that they are causally related.

The reproductive rates discussed so far described the response of the individual females in the population to changes in population characteristics over time. However, since the proportion of females in the population has varied over time due to differential harvest rates, the preceding information does not indicate the rate of addition of lambs to the population as a whole. This can be determined by calculating the number of lambs per sheep in the populations.

The reproductive rates of the population as a whole follow a pattern similar to that of the ewes. Figure 38 shows the reproductive output of the entire population over time. From 1894 to 1928 the production of lambs tended to increase linearly. The much higher rates in a few of the early years probably resulted from purchases of new breeding stock, skewed sex ratios, or changes in the land holdings. After 1928, the lamb production declined steadily until the mid-1940's, when the rate oscillated wildly around an average value of about 0.32 lambs per sheep. The decline in lamb production over time is given by the non-linear regression formula:

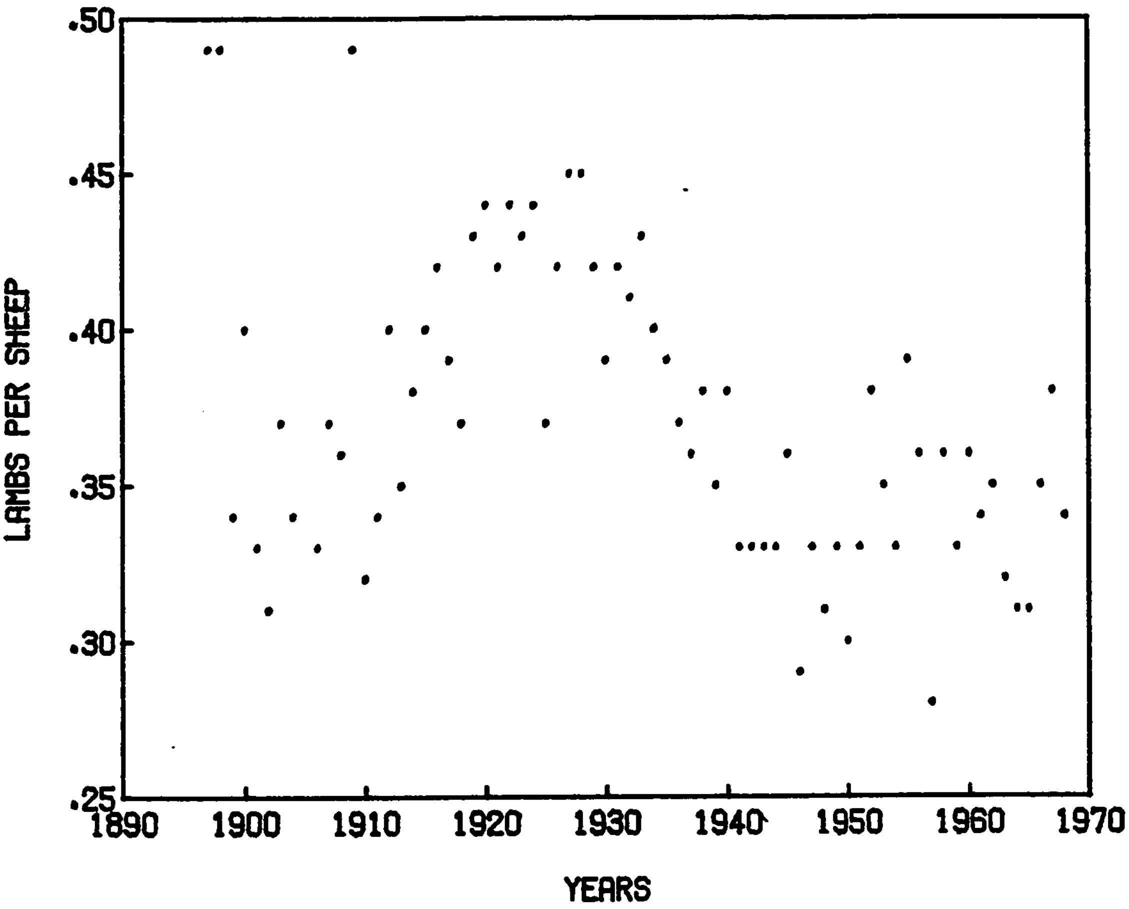

Figure 38. Lamb productivity of the entire sheep population of the Ganadera over time.

$$LP = +0.448(T)^{-0.086} \qquad (8)$$

where LP is the lambs per sheep, and T is the number of years after the peak in 1927. The regression is significant at P=0.00001, with an R-square of 0.49.

Lamb production by the entire population is inversely correlated with population density. The regression formula is:

$$LP = 0.4449 - 0.12(D) \qquad (9)$$

where LP is the same measure of lamb production, and D is the sheep population density. The regression is significant at the P=0.0043; however, the correlation is weak, with an R-square of only 0.20. The lack of close correlation is probably due to improved management during the period of initial increases in density (1894 to 1935), which resulted in an increasing proportion of lamb survival. In the period after stabilization of the herd size, the sex ratios were changed to favor the ewes, thus further reducing the correlation with absolute density.

8.3 Mortality Patterns

Sheep are lost from the population through natural mortality and harvesting of lambs and yearlings for meat. For the purpose of this analysis, both types of loss will be considered mortality.

8.3.1 Harvest Mortality

The rate of harvesting is a function of management decisions in response to changes in the population growth, natural mortality, economics, and politics. The harvest rate for the sheep population of the Ganadera has varied greatly since the establishment of the herds. In Figure 39 the harvest rate, measured as the percent of the herd

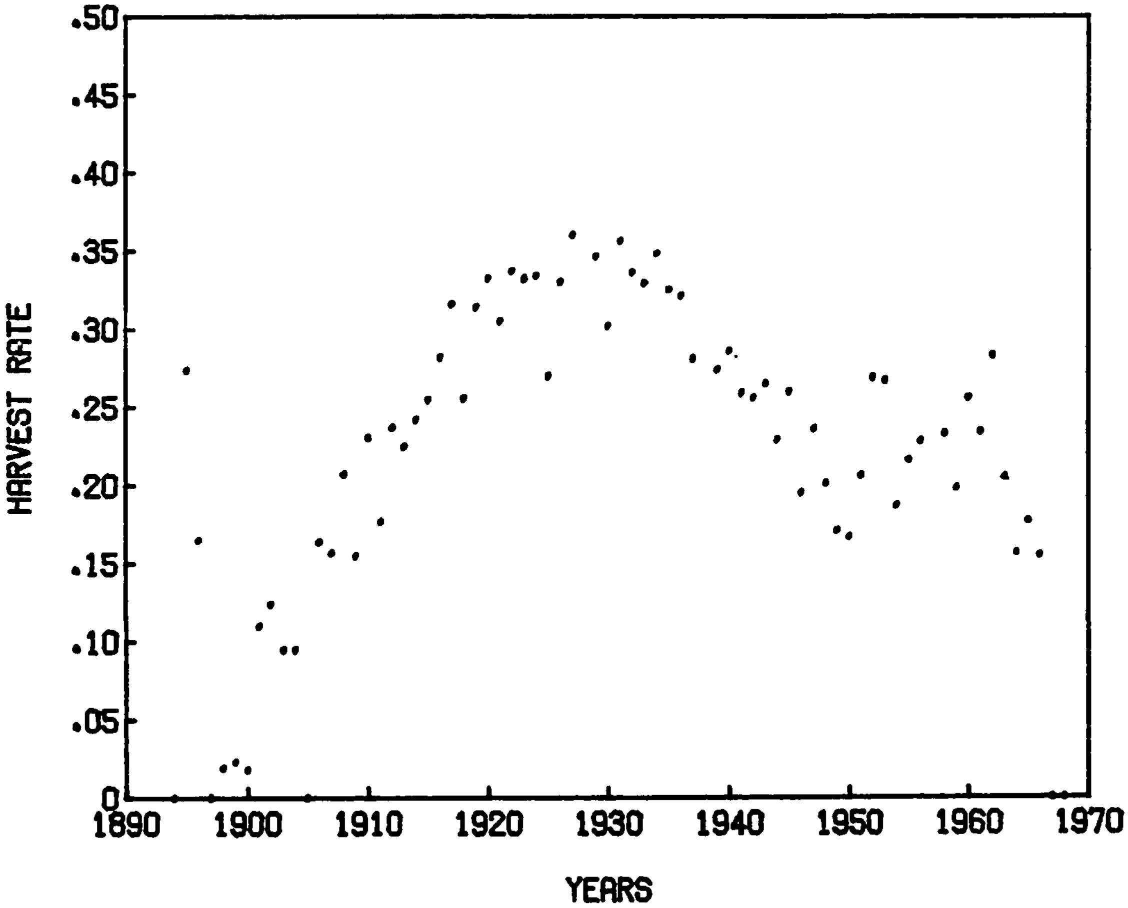

Figure 39. The harvesting rate applied to the sheep population of the Ganadera over time.

harvested annually, is plotted over time. The harvest rate initially increases linearly with an increase in sheep density. Then in 1921 the harvest rate stabilized at approximately 33% of the herd per year, until 1936. After the peak in population densities in the mid-1930's, the harvest rate declined consistently until the mid-1940's. I interpret this as a deliberate attempt to maintain herd numbers and wool production during a period in which the carrying capacity and reproductive gain were declining due to excessive stocking rates. In the mid-1940's when the deterioration of the ranges became clearly apparent (Erasmo 1972), the harvest rates no longer declined, but still varied greatly from year to year.

The regression of harvest rate with density is significant, with $P=0.0001$ and a R-square of 0.46. The harvest rate increased gradually with increase in densities, given by the regression formula:

$$H = 0.067 + 0.309(D) \qquad (10)$$

where H is the harvest rate, and D is the sheep density. However, the harvest rate was never high enough to maintain a constant herd density.

8.3.2 Natural Mortality

Natural mortality includes both density-dependent mortality, which is affected by harvest mortality, and density-independent mortality, which is not. Even in the period when the sheep population was expanding exponentially, and the population was well below carrying capacity, the total mortality rate, largely density-independent, never dropped below 4% (see Figure 40). After 1915, natural mortality decreased as the harvest rate increased (see Figure 41). By 1955 the natural mortality had declined to an annual rate of only 6%. However, with the decrease in the harvest rate after the population reached K, the natural mortality again increased, peaking in the mid-1950's. Natural mortality remained high throughout the 1960's when the harvest rate was intermediate, and the population was at or a little above carrying capacity.

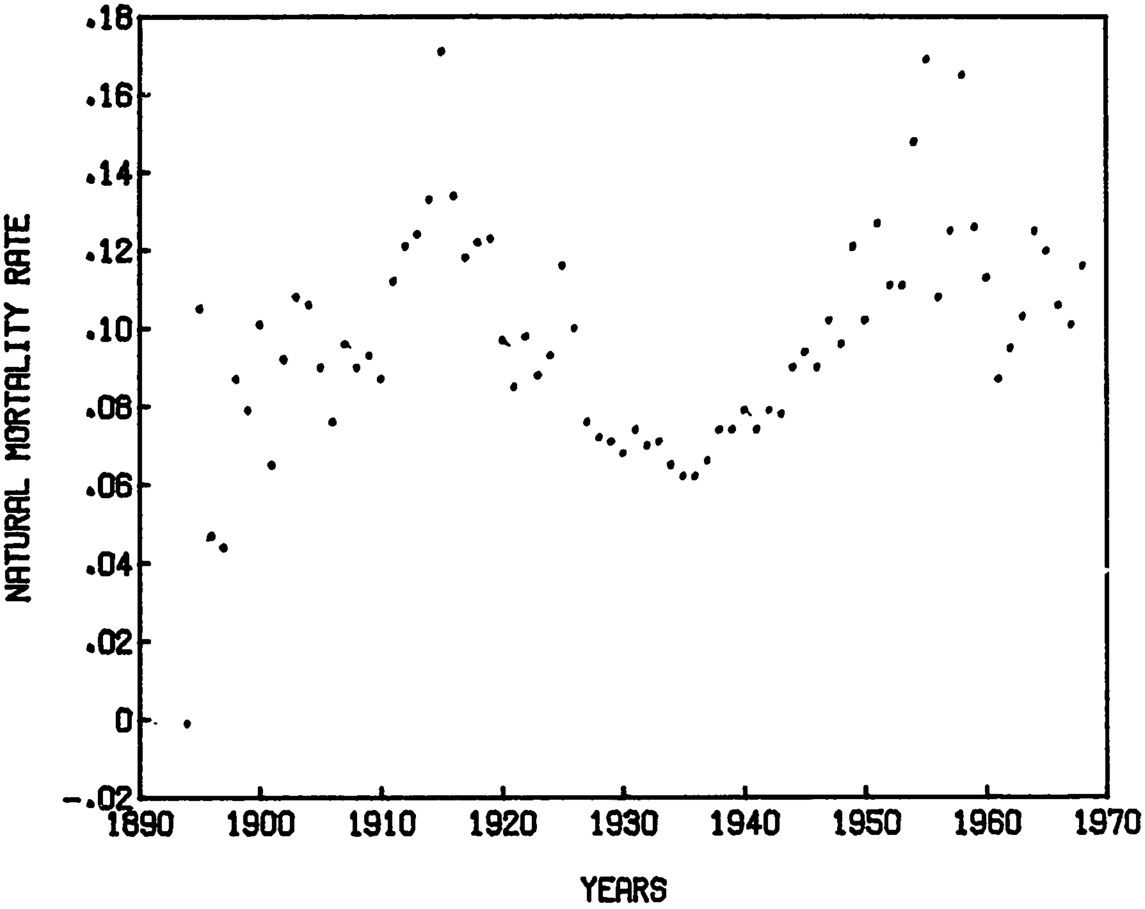

Figure 40. Natural mortality rate of the sheep population of the Ganadera over time.

8.3.3 Total Mortality

Total mortality consists of natural mortality plus harvest mortality, and is influenced by the annual rate of production, or reproductive gain, since this affects the size of the population from which the mortality is drawn, and hence the relative magnitude of the loss.

Total mortality, low in the initial years of introduction, increased to about about 45% per year in 1917 and was maintained at this level to 1931. Then it slowly declined, as reproduction declined, until 1950, when it was about 40%. Subsequently there has been no long-term trend as the factors of expropriation, economics weather, and politics have interacted in an erratic fashion. In Figure 39 the total mortality rate is plotted over time.

The combined mortality rate is highly correlated with population density. During the period from 1894 to 1935, when the population was growing in a logistic-like manner, the mortality increased linearly with increases in density. The regression formula is:

$$M = 0.1201 + 0.4773(D) \qquad (11)$$

where M is the combined natural and harvest mortality, and D is the population density. The regression is significant at P=0.0001, and the R-square is 0.732.

Once the population had reached carrying capacity, from 1935 to the mid-1960's tne mortality rate declined in conjunction with declining reproductive rates (see Figures 37 and 38). Mortality was no longer functionally related

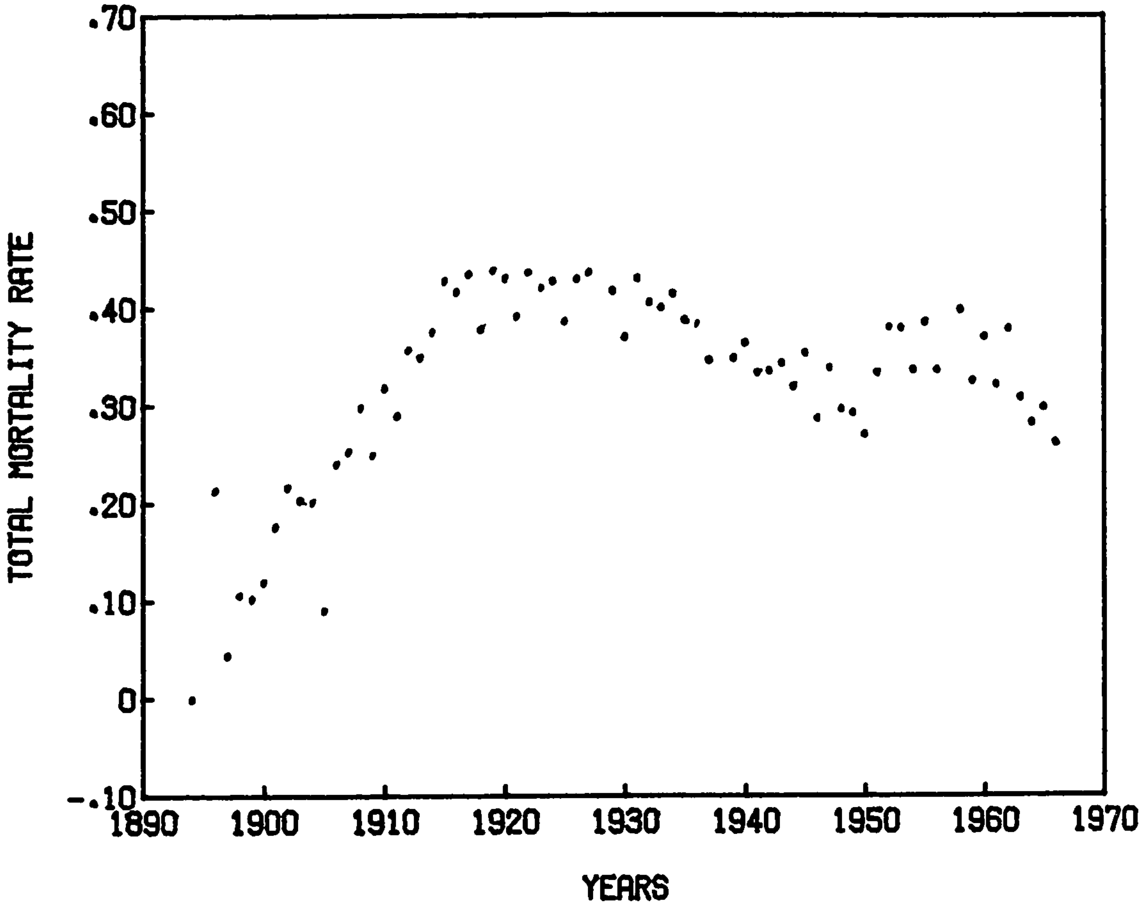

Figure 41. Total mortality rate, natural plus harvest, for the sheep population of the Ganadera since introduction in 1894.

to density, which was constant, but rather was a function of the reproductive rates.

It is apparent from this data that natural mortality and harvest mortality are highly correlated. In the early stages of population growth, both increased rapidly. However, from 1925 to 1966, the two were clearly compensating. When harvest was high, natural mortality was low, and vice versa (see Figures 39 and 40). In Figure 42 the natural mortality is regressed as a function of harvest mortality over the period from 1930 to 1966. It is clear that as the harvest declines, the natural mortality rate increases. However, the correlation between the two rates appears to be reduced by a lag time in response of natural mortality to a decline in harvest mortality. For example, as the harvest rate began to

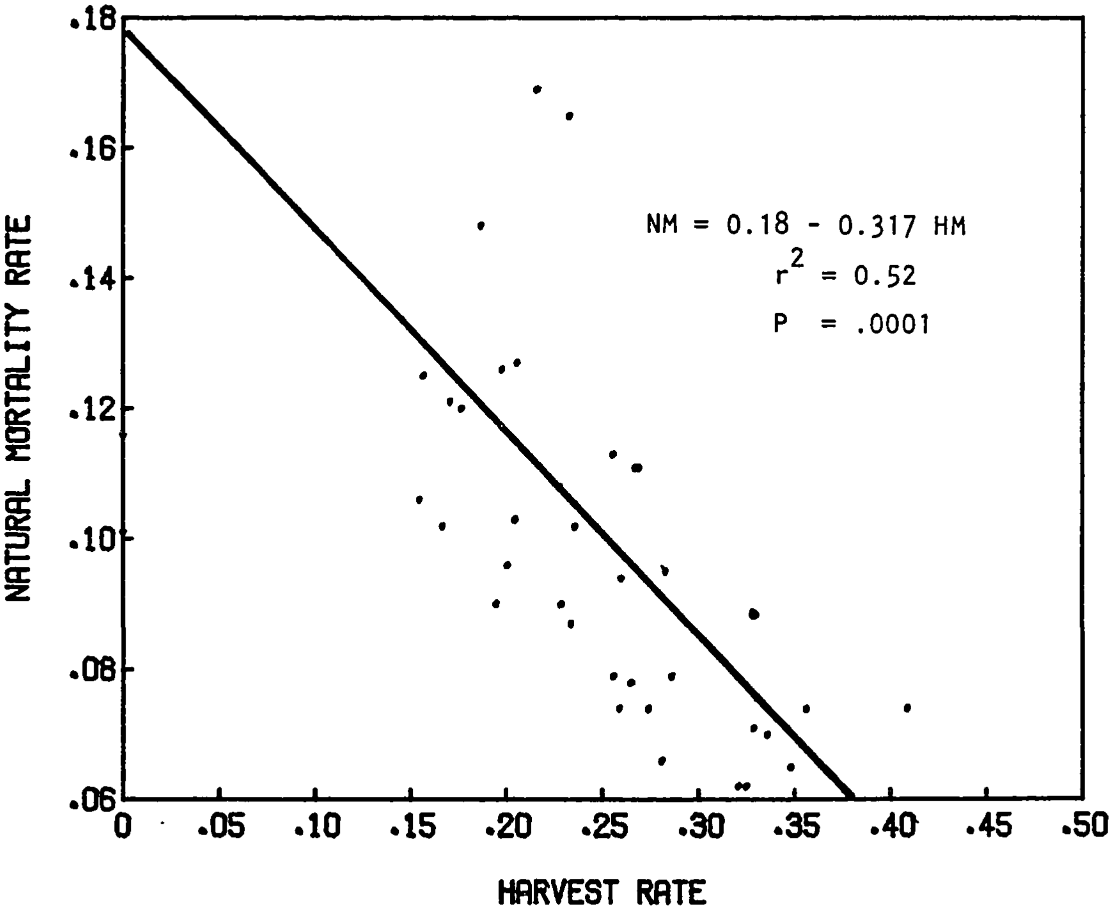

Figure 42. The correlation of harvest and natural mortality rates, over the period 1930 to 1966.

decline around 1930, the natural mortality rate continued to decline. The rate of decline was reduced, but the decline continued. It was not until 1936 that the natural mortality rate began to increase, some 6 years after the decline in harvest. This suggests that the relationship between natural mortality and harvest mortality depends on a reduction of carrying capacity of the range resulting for an overshoot in carrying capacity. The reduction in carrying capacity is not instantaneous; in this case it took six years of overgrazing to reduce the quality of the diet sufficiently to cause an increase in the rate of natural mortality. This is the model of damped oscillations of ungulate populations proposed by Caughley (1977), resulting from an interaction of the ungulate population with the plant resource.

8.3.4 Causes of Mortality

Most natural mortality of sheep in Magallanes is related to the reduction of forage availability and quality in the winter. However, the actual causes of natural mortality have been poorly documented.

In an unpublished study of lamb mortality, the Instituto de Investigaciones de Agropecuarias, Punta Arenas, Chile, reported that starvation was the principal cause of mortality. They found that in the cases in which the cause of death was established, the causes of death were: starvation - 55%, disease - 26%, and predation 18%.

In adult sheep, winter starvation and deaths related to poor physical condition are considered to be the major cause of mortality. In the present study area, starvation was estimated to account for over 50% of the average annual mortality, and accidents resulting from weakened condition accounted for another 25% (C. Bristilio per. comm.). The remaining mortality was attributed to disease, other non-condition related accidents, and some minor predation.

In general, predators can be discounted as an important mortality factor, since they have been generally eliminated from the prime sheep range. The puma is still an important predator in localized areas on the continent. Especially in the scrublands in the precordillera. But these areas account for only a small part of the total sheep range. Most carnivores in the region are scavengers that thrive on the numerous carcasses resulting from accidental deaths, disease, starvation, etc., and the puma is not found on the island.

8.4 Regulation of the Sheep Population

The carrying capacity of the range is clearly the ultimate factor limiting the growth of this sheep population. This conclusion is based on the observations of the population characteristics, presented in the preceding sections, and summarized below:

1. Density-dependent mortality and natality rates through the expansion of the population to K.
2. Compensatory natural mortality and harvest mortality once K has been reached.
3. An increase in population size accompanying improvements of the range forage resource.
4. A reduction in population size resulting from a deterioration in range conditions.
5. Substantial mortality caused by starvation.
6. Lack of identified density-independent factors that could account for the logistic-like growth patterns (such as weather or predation).

It should be noted that the yearly variability in weather influences the food supply and carrying capacity of the habitat, thereby affecting fecundity and mortality rates. The result of such changes in the mortality and fecundity rates would be short term, possibly random fluctuations in the population size. If sufficient weather records were available, it might be possible to correlate short term changes in the population with changes in the weather. However, such records are not available. In any case, weather should be considered a proximate facor in population regulation, while the carrying capacity of the habitat, dependent on the forage resource, is the ultimate factor.

Even though the sheep population is under human management, it is still subject to natural selection in addition to artificial selection. McCullough (1978:302) stated that such "...large herbivores are K-selected i.e. over evolutionary time they have been subject to selection for ability to compete for resources in a density-dependent environment." One population characterisitc resulting from such selection, coupled with the low reproductive rates of sheep, is a "high degree of tracking of carrying capacity" (McCullough ibid).

The growth of the sheep population after introduction into Magallanes province closely follows the model proposed by Riney (1964). He stated that "introduced populations of large herbivores, if undisturbed, normally follow a pattern of adjustment to the new environment which consists of a single eruptive oscillation." Caughley (1970) refined the model by defining four hypothetical stages: 1) initial increase to the initial peak, 2) initial stabilization stage until significant decline due to forage depletition, 3) decline, and 4) post-decline. Caughley also reviewed the published accounts of such population growth in ungulates. In the following section, the growth pattern of the sheep population will be related to the interaction of the birth and death rates presented in the earlier sections, with special reference to the hypothetical stage of the Riney model.

The first two stages in Riney's model can be combined into the common logistic growth model. For the sheep population, this stage covers the period from 1894 to 1938. The classical interpretation of the logistic model assumes linearly declining reproductive rates, and linearly increasing mortality rates as the carrying capacity, K, is approached at stabilization (Wilson and Bossert 1971). However, in the sheep population the initial decline in the growth rates over the period from 1905 to 1917, after the exponential growth phase, is attributable to rapidly increasing mortality (see Figure 41), since the reproductive rates(actually measured as the recruitment of lambs to the two month old age class) are also generally increasing. During the stabiiization stage (1918 to 1938) the termination of population growth was affected by a decline in the reproductive rates (see Figure 38) while the total mortality rates remained fairly constant. During this period, an apparent attempt to maintain population growth, by a reduction in harvest rates, was thwarted by an increase in natural mortality.

As predicted by Riney's model, the peak in sheep numbers was not maintained, even with the reduction in harvest rates, and the population entered a period of gradual decline. Natural mortality compensated for the lowered harvest, rates however there appears to be a lag time of some six years before the natural mortality totally compensates. Overall, the mortality rates actually decline during this period. The principal factor in the decline in this period is the reduction in reproductive rates, which went from the peak in 1924 of 0.45 lambs per sheep to 0.35 lambs per sheep in 1948. While the cause of this decline is not fully documented (see section 8.2), the reduction in range condition that generally results from a population held above carrying capacity (Caughley 1970 and 1977, and Stoddart *et al.* 1975) undoubtedly played an important role.

The sheep population responded to the environment like a natural, free-living population through the first three stages of Riney's model. However, beginning in the mid-1950's this 'natural period' ended as the herd and the range were much more intensively managed. As soon as management took a more effective hand, the interaction of the parameters is much more complicated. Sex ratios, harvest rates, and age structure were changed from year to year in response to economic conditions and changing management goasl. However, the data indicate that even in this period, the population was still ultimately limited by the carrying capacity of the habitat.

CHAPTER 9

Interactions of Guanaco and Sheep Populations

Two populations may or may not affect each other, and if they do, the result may be beneficial, neutral, or adverse. At least four types of interactions have been documented for ungulate populations: protocooperation, when the interaction is favorable to both species, but is not obligatory (i.e. rotational grazing by African ungulates as described by Bell 1971); neutralism, when neither species is affected (i.e. nearly complete separation of range use by deer, elk, and cattle as described by Mackie 1970); amensalism, also referred to as "unilateral competition", when one species is inhibited, but the other is unaffected (i.e. summer use by cattle of elk winter range, as described by Nagle and Harris 1966); and competition, when each species inhibits the other.

The purpose of this section is to evaluate the interactions of sheep and guanacos on the range; specifically to determine the extent to which sheep and guanacos share the forage and habitat resources, and the extent to which interactions with sheep have changed the forage and habitat use patterns of the guanaco.

9.1 Competition

By definition, competition occurs when two animals or populations share an identical resource, and that resource is insufficient for both. Moreover, when in competition, the presence of each animal reduces the fitness and/or equilibrium population size of the other animal. Competition can occur when the resource is not limited if social interactions such as dominance relations exclude one species from the resource. This type of competition is called "interference competition", while the more direct competition that results from joint use of the same resource has been termed "exploitative competition" (Schoener 1971).

9.1.1 The Approach to the Study of Guanaco-Sheep Interactions

The interactions of sheep and guanaco populations were analyzed by comparing food habits and habitat use of both species under varying degrees of population interaction. First, the aboriginal niche of the guanaco was reconstructed from historical accounts. Second, the current niches of the guanaco and sheep populations were determined from studies of habitat use and food habits. Habitat use by the two species was described in general for the entire region, and the intensive study area. The food habits analysis was confined to the intensive study area. Third, the impact of the sheep on the guanaco population was analyzed by comparing the aboriginal (fundamental) and current (realized) niches of the guanaco, and the niche shifts that occur with seasonal changes in interactions with sheep. Finally, the dynamics of competition were evaluated through an analysis of the niche overlap and direct population interactions.

9.1.2 The Competition Hypothesis

Competition between sheep and guanacos for the forage resource is thought to be the ultimate factor currently controlling the level of the guanaco population of the study area. The following hypotheses are tested in the subsequent sections:

1. The guanaco has been restricted in habitat use by the introduction of sheep through a process of competitive exclusions (the realized niche is a subset of the fundamental niche).
2. Competition has affected the diet of the guanaco.
3. The guanaco has been excluded from habitats used in common with sheep except those that provide forage dimensions that allow dietary separation between guanacos and sheep.
4. The guanaco and sheep populations of the study area have reached a competitive equilibrium, and will coexist indefinitely, unless manipulated by man through direct means by changes in the environment.

9.2 The Aboriginal Guanaco Niche

The aboriginal niche of the guanaco, i.e. before the introduction of domestic sheep, has been assimilated from the few published accounts of guanaco life history.

Previous to the present study, the information on the food habits of the guanaco was primarily qualitative. Dennier de la Tour (1954) and Romero (1927) commented that the guanaco is a generalist herbivore that readily eats all the range plants, with a general preference for grasses. Bridges (1948) noted that guanacos along the Beagle Canal ate considerable amounts of browse from the evergreen beech trees, as grass was extremely limited in abundance. Other authors writing about the guanaco in general throughout Patagonia notably Stassen (1916) and Cabrera and Yepes (1940), described the diet as consisting of grasses of the pampa.

The information of the habitat preferences of the guanaco is more extensive, since many authors recorded sightings of guanacos. Before the introduction of sheep, the preferred habitat of the guanaco appears to have been the open grasslands of Patagonia. The early naturalists all indicated that the highest densities of guanacos were found on the pampa (Darwin 1845, Rogers 1877, Prichard 1902, Romero 1927), especially on the fertile, moist river plains. Rogers (1877) counted over 5,000 guanacos in one day on the pampa, and calculated the population to be over 1.5 million guanacos in the area south of the Rio Santa Cruz in Argentina. The scrublands in the foothills of the Andes at the fringes of the grasslands also supported large numbers of guanacos, but this was definitely secondary habitat (Darwin 1845).

Forested areas apparently did not support large guanaco populations. Prichard (1902) noted that he saw no guanacos in the forested regions in all his travels through Tierra del Fuego. Other authors either inferred that the guanaco was not abundant in the forest (Osgood 1943, Romero 1927), or noted only slight use of the forest habitat (Cardozo 1954, Dennler de la Tour 1954). The observations of Cardozo (1954) and Dennler de la Tour (1954) are particularly interesting, since even though by 1954 most of the guanacos of the pampa had already been eliminated, these biologists still considered the forest to be only marginal habitat for the remaining guanaco populations. Bridges (1948) was the first to suggest that the forest was adequate guanaco habitat, although inferior to the grasslands of central Isla Grande.

From these observtions, it is possible to reconstruct an idealized distribution guanacos along a vegetation ecocline. Figure 43 illustrates the reconstructed guanaco densities along the vegetation-moisture gradient, extending from the cool and damp on the left (west), to warm and dry on the right (east). This ecocline roughly represents the transition from the wet, temperate

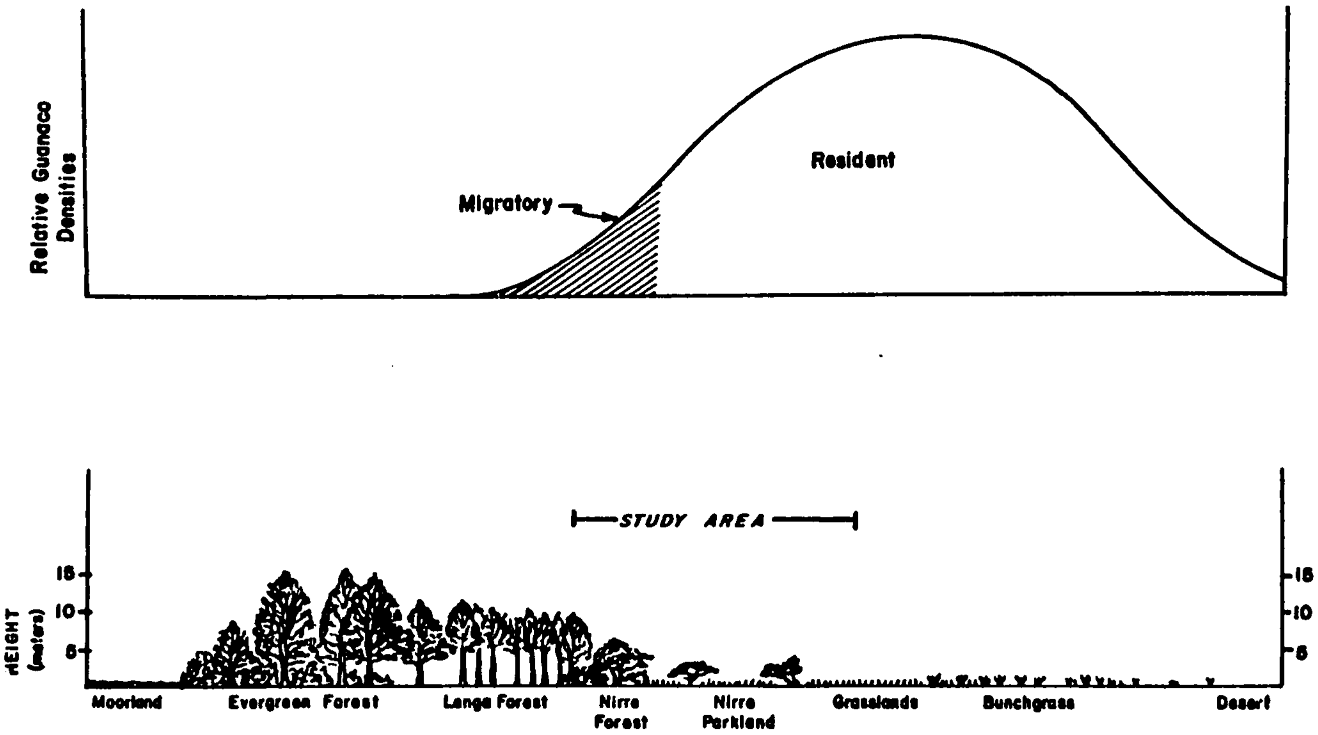

Figure 43. Reconstructed guanaco densities along the habitat ecocline of southern Patagonia.

evergreen forests and moorlands on the west side of the South American continent to the coastal deserts in the east. The intensive study area extends from the eastern edge of the evergreen forest to the central portion of the grasslands. The grasslands in the ecocline are equivalent to the grasslands in the Rio Grande Basin of the study area (see Figures 6, 11, and 12).

9.3 Current Habitat Use by Guanacos and Sheep

Schoener (1974b) noted in his review of resource partitioning and competition, that differential use of the habitat is most often the dimension of the niche that separates similar species. Numerous studies have shown that this is also true for ungulates (Mackie 1970, Lamprey 1963, Bell 1971, and Stoddart *et al.* 1975).

Current habitat use by both guanacos and sheep was evaluated by calculating population densities supported in the different macro-habitat types in the region and the study area. The guanaco densities were calculated on the basis of the census data, presented in an earlier section, and aerial surveys. The sheep densities were determined from the stocking records of the estancia and the government agricultural agencies. The distribution of range use within the macro-habitats was determined by field observations.

9.3.1 Regional Habitat Use by Guanacos and Sheep

Sheep herds have been successfully established in all the economically viable sheep habitats of the province, with the resultant concentration of sheep on what was the most productive part of the guanaco range. Sheep are now grazed in all habitats represented in the ecocline in Figure 43 that are east of the evergreen forest. The nirre forest zone is suitable for sheep summer range; the actual extent of sheep grazing depends on the availability of winter range in the surrounding lands. Attempts to establish sheep herds in the forested zone have been generally unsuccessful. Only small herds are currently grazed in the forested parts, and these rely on small clearings interspersed throughout the forest.

Sheep numbers are also low in the dry, desert-like portions of the ecocline, along the eastern coast of the continent. However, this habitat type is not extensive in Magallanes.

The distribution and density of the guanacos in the various habitat types within the province has changed dramatically since aboriginal times, as represented in Figure 43. The current distribution of guanacos was given in Figure 16. If we combine the information from this distribution map, with the map of vegetation types, we note that the present guanaco population is concentrated at the interface of the forest and grasslands, in the forests of the south and west, and at the eastern (dry) fringes of the sheep range. Thus the guanaco survives largely in marginal habitats, with the major former habitat now being preempted by sheep.

9.3.2 Habitat use by guanacos and sheep on the study area

During the present study, both guanacos and sheep were widely distributed throughout the study area, and both species utilized all macro-habitat types to some extent. However, each habitat characteristically supported different relative densities of the two species.

The habitat use patterns for the sheep and guanacos on the study area are given in Figure 44, which plots the densities of the non-migratory guanacos and sheep across the pampa-forest ecocline. This figure represents the

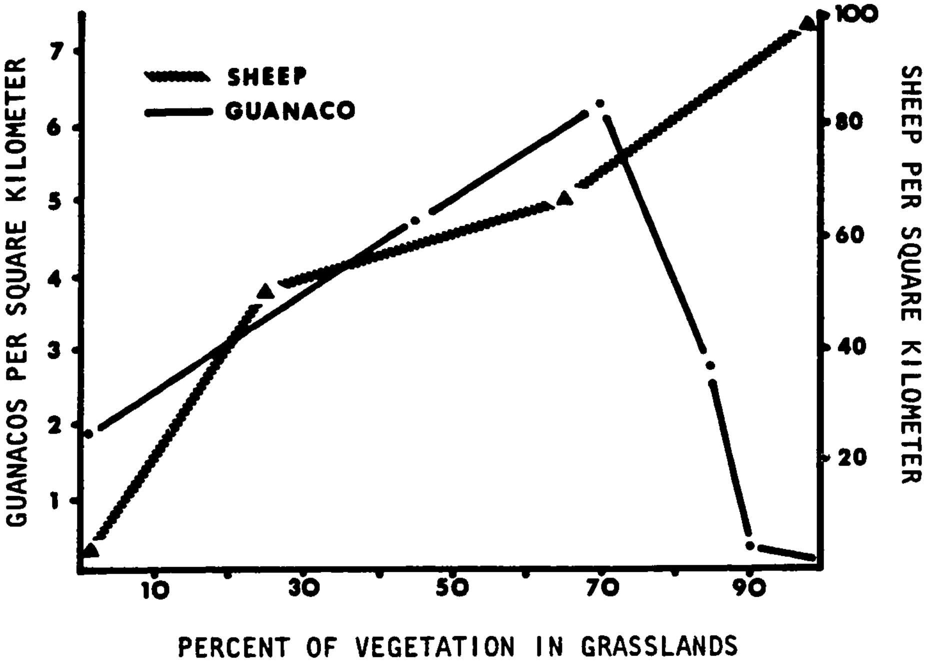

Figure 44. Guanaco and sheep densities along the habitat ecocline in the intensive study area.

section of the ecocline in Figure 43 from the grasslands to the edge of the continuous lenga beech forest. Since the sheep used the area seasonally, the sheep densities were corrected to represent annual average densities. Furthermore, if the migratory guanacos were included, the guanaco densities in the forest end of the continuum would increase from 1.8 to about 6.0 guanacos per square kilometer.

The guanaco densities were greatest at the ecotone between the forest and the open grasslands in the southern part of the study area (see Figure 3). Guanacos were seldom seen more than one or two kilometers from the forest, having apparently been almost completely excluded from the open pampa.

Sheep densities were greatest on the open pampa, and decline almost linearly with the increase in forest cover. No sheep are found to use the continuous beech forest area south of the study area.

Vegetation, not topography, appears to be the basis of range partitioning between sheep and guanacos, since both sheep and guanacos readily graze and travel on even the steepest terrain. Stoddart *et al.* (1975) reported that the domestic sheep is second only to the goat in the ability to distribute itself and to graze on all terrain types. Furthermore, the herding of sheep, the use of fenced pastures, and rotational grazing insured that the sheep utilized all the suitable topography of the region.

9.3.3 Seasonal Sheep Habitat Use and Guanaco Response

Both direct observation and food habits data indicate that where guanacos and sheep were found together the guanacos used their habitat differently than when alone. With sheep competition, both in the summer and winter, the guanacos utilized the forest habitat to a greater extent than when sheep were few or absent. This does not seem to be due to a general reduction in the quality of the grasslands or weather patterns, since the sheep should also respond to such changes in the habitat, but they did not.

The proportition of the guanaco population oberved on the pampa decreased when the area was also occupied by sheep. A comparison of the guanaco habitat use on the sheep winter range in the northeast section of the study area (see Figure 47) demonstrates this shift. The estimated guanaco densities were at least three times as great on the pampa as in the forest during the summer, when sheep were absent from both habitats (see Table 28). However, in the winter when sheep were present on the pampa, the guanaco densities were greater in the forest than on the pampa. The winter ratio of the densities of forest to pampa were 1.3:1 in 1972, 2.4:1 in 1973, and

Table 28. Summer guanaco densities*for forest and pampa habitats. Data is from Raedeke (1978) based on the trasect censuses.

Year	Forest	Pampa
1972	0.38 ± 0.23	1.42 ± 0.40
1973	0.13 ± 0.09	1.19 ± 0.28
1974	0.31 ± 0.13	1.29 ± 0.33

* The densities are given as guanacos per square kilometer ± 95% condifence interval.

1.6:1 in 1974. A similar shift was observed on other seasonal range types.

Data on the food habits show that sheep eat about the same diet whether they share the range with guanacos or not, but when sheep are present guanacos obtain more of their food in the forest (see Tables 29 and 31).

9.4 Food Habits of Guanacos and Sheep

The second component of the niche to be considered is that of food habits. Schoener (1974b) found that 78% of sympatric species that have been studied partitioned the environment on the basis of the food habits component of the niche. Various studies of ungulates also have shown that sympatric species can coexist by using different food types (i.e. buffalo and antelope, Buechner 1961; various African antelope, Lamprey 1963; cattle, sheep and deer, Stoddart *et al.* 1975).

In the following section, the diets of guanacos and sheep, which had a free choice of diet on the range, will be described. Two methods were used to determine diets. First, rumen samples collected from guanacos throughout the study area were separated by plant species to provide a detailed description of seasonal diets. The rumen samples were collected from guanacos from ranges with and without sheep. Second, the diets of sympatric guanacos and sheep were determined for comparative studies through fecal analysis. The pellets were collected from the northeastern section of the study area, approximately 10 kilometers northeast of the section Rio Grande. This area was used by sheep and resident guanacos throughout the year, although the summer sheep densities were low.

The production of new plant growth is highly seasonal in the temperate grasslands of Patagonia. In Magallanes, the annual growth period is limited to the spring, from September to mid-December (IREN 1967). During the course of the year, most of the palatable range forage is consumed by the herbivores on the range. A comparison of the dry weights of clipped samples from inside and outside of a 100 meter-square exclosure showed that 90 to 95% of the grass and grass-likes, and virtually all of the forbs were consumed by the end of the grazing season. However, the browse was much less fully utilized. Below one meter in height, about 30 to 50% of the browse was consumed, and above one meter, the utilization was negligible. The sheep and guanaco grazing in the summer on the sheep winter range, apparently did not greatly reduce the fall forage supply, since fall clippings were not measurably different from inside and outside the exclosure.

It seems reasonable to assume that the seasonal changes in the density of sheep on the range, and the availability of the forage, produce changes in the intensity of competition between the herbivores. Competition presumably increases as the forage supplies are reduced in the winter (or in fall on the summer range areas).

9.4.1 General Food Habits of Guanacos

Twenty-four guanaco rumen samples were collected, representing all months of the year except January, February, and July. Samples were collected from both sexes and all age classes, and came from sub-populations which varied with respect to the amount of concurrent competition with sheep.

The results are summarized in by sample in Table 29, and by month in Figure 45. In both cases, the plant species have been combined into the plant life forms of grasses (including grass-likes), browse, epiphytes, lichens, fungi, and forbs. The actual plant species identified in the rumen samples, and the percentage of the samples in which they were identified, are given in Table 30.

Forty plant species were identified in the samples. With the exception of the grasses, and some succulent forbs, the majority of the species were readily identifiable. However, less than 10% of the grass and grass-like material was identified to species, so it seems likely that some grass species were eaten but not identified in the samples. Furthermore, if all the grass material had been identified to species, the percentage of

Table 29. Food habits of the guanaco of the study area, as determined by rumen analysis. The tabled values are percent of the total sample. The range types listed are: W = winter; S = summer.

Number	Month Year	Range type	Season	Grass & grasslike	Browse	Lichens	Epiphytes	Forbs	Fungi
G7	3/73	S	S	2.4	95.2	1.3	-	1.1	-
G8	3/73	W	S	37.9	24.3	2.2	25.7	4.8	8.9
G9	4/73	W	S	37.8	8.0	0.2	13.7	2.5	37.8
G10	4/73	W	S	82.5	2.1	0.5	11.5	3.7	-
G14	5/74	W	S	75.3	4.0	0.4	10.0	10.2	0.1
G15	6/74	S	W	76.1	14.9	5.4	0.2	3.3	-
G16	6/74	S	W	54.1	16.2	3.8	tr	25.4	-
G17	6/74	S	W	42.2	15.6	37.5	0.6	4.0	-
G1	8/72	W	W	89.2	1.6	tr	2.5	6.7	-
G3	8/72	W	W	82.2	9.7	tr	tr	7.4	-
G11	8/73	W	W	64.6	7.8	tr	20.4	7.2	-
G12	8/73	W	W	91.0	2.8	-	-	6.1	-
G13	8/73	W	W	96.5	3.8	tr	tr	3.1	-
G2	9/72	S	W	79.3	10.3	0.5	2.4	7.4	-
G18	10/74	W	W	54.2	10.8	-	33.4	1.6	-
G19	10/74	W	W	93.2	2.1	-	tr	4.7	-
G20	10/74	S	W	91.0	4.5	tr	1.9	2.0	-
G4	11/72	S	W	49.9	30.1	1.2	1.0	17.6	-
G5	11/72	W	W	26.7	5.0	0.9	10.0	57.4	-
G21	11/74	W	W	63.7	29.4	tr	4.9	1.9	-
G6	12/72	W	W	58.8	30.5	10.7	2.9	5.1	-
G22	12/74	W	W	58.9	3.7	tr	0.4	36.3	-
G23	12/74	S	S	59.4	3.0	tr	tr	37.6	-
G24	12/74	S	S	75.7	5.8	tr	5.4	13.2	-

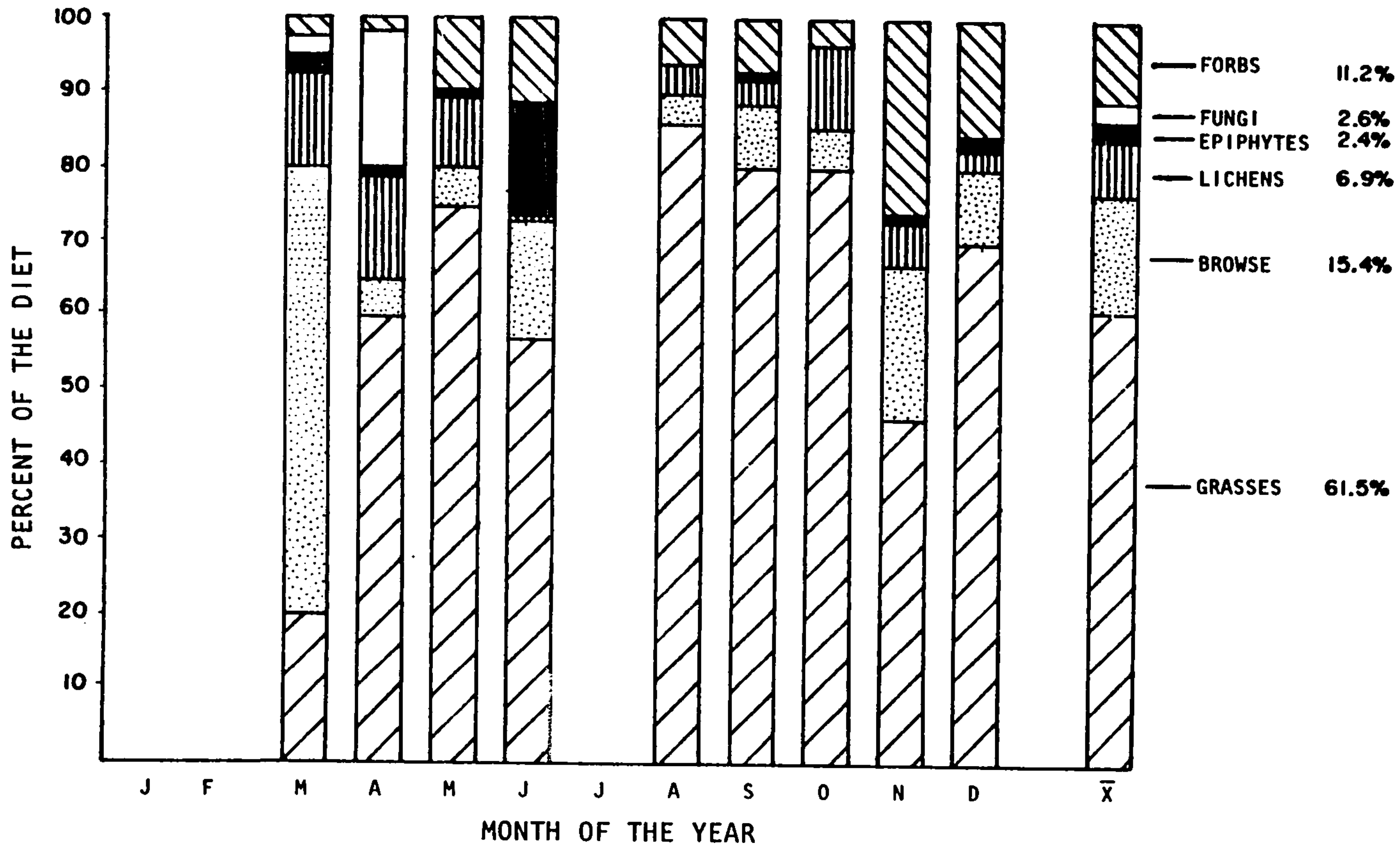

Figure 45. Monthly and annual food habits of the guanaco, determined by rumen analysis.

Table 30. Plant species, with percent of occurance, in the diet of guanacos of the study area on Isla Grande, Chile.

Common Spanish Name	Scientific Name	Frequency (%)
Tree Species:		
Nire	Nothofagus antarctica	100
Lenga	Nothofagus pumilio	50
Coigue	Nothofagus betuloides	4
Shrub Species:		
Calafate comun	Berberis buxifolia	96
Romerillo	Chiliotrichium diffusum	50
Michay	Berberis ilicifolia	42
Murtilla	Espetrum rubrum	29
Mata gris	Senecio patagonicus	13
Mata verde	Baccharis patagonica	8
Calafate enano	Berberis empertrifolia	4
Chaura	Pernettya mucronata	4
-	Berberis heterophylla	4
Epiphyte Species:		
Clavel de viento	Mesodendrum punctulatum	100
Fern Species:		
-	Blechnum penna-marina	25
Funji Species		
Dihuenes	Cyttraia darwinii	29
Lichen Species:		
Barbara del viento	Usnea spp.	75
Grass and Grasslike Species:		
Junquilla	Marsipperumum grandiflorum	38
Festuca or coiron	Festuca gracillima	38
-	Deschampsia antarctica	18
Festuca	Poa pratensis	13
-	Agrostis spp.	8
-	Carex decidua	8

Table 30. Continued.

Common Spanish Name	Scientific Name	Frequency (%)
Festuca	Festuca magellanica	8
-	Geum magellanica	4
-	Carex sp.	4
Forb species:		
Chicoria	Taraxacum officinale	37
Cadillo	Acaena magellanica	21
-	Codonorchis lessonii	21
Cadillo	Acaena pinnatifida	17
Vinagrillo	Rumex acetose-la	17
Bolsita del pastor	Capsella bursa-pastoris	13
-	Phleum alpinum	12
Cadillo	Acaena ovalifolia	8
Mogote	Azorella trifucata	8
-	Ranunculus peduncularis	8
Frutia del Diablo	Gunnera magellanica	4
Flor de la estrella	Perezia recurvata	4
-	Colobanthus subulatus	4
-	Senecio acanthyfolius	4
-	Osmorrhiza obtusa	4

occurence of the different species would most likely have increased.

In general, the consumption of any forage species is closely related to its phenology and availability. Guanacos ate browse and forbs when they were at their peak in abundance and most palatable in the spring and early summer. The fungi, lichens, and epiphytes were eaten in the fall when they were most readily available. In apparent contrast to this general rule, grasses were eaten least in spring and early summer when at their peak of new growth and abundance. Evidently the guanacos prefer new growth of forbs and browse to new growth of grasses.

However, the principal food of the guanaco was the grass of the pampa. Approximately 60% of the annual diet consisted of grass and grass-likes. In December and January at the beginning of summer, grasses made up about 60% of the diet, but during the late summer months, the grass consumption declined to less than 20% by March. Grass use increased to its maximum of 85% of the diet in winter (July to October). From late winter through spring the percentage of the grass in the diet declined gradually with a concurrent increase in the consumption of forbs and browse.

Nine grass species were identified in the rumen samples. The most important grasses, on the basis of frequency of occurence in the samples, were the "coiron" or fustuca bunch grasses(*Festuca gracillima*, and *Festuca magellanica*). These species were identified in 40% of the samples.

The second most important component of the diet was the browse, from both trees and shrubs. This forage class constituted 15.4% of the total annual diet. The consumption of browse was highest in the spring and summer when the deciduous trees had leafed out, and many of the shrubs were flowering. The lowest consumption of browse was in the winter when the trees has lost their leaves. The winter browse consumption consisted of almost entirely evegreen shrubs such as *Berberis buxifolia*, *Berberis illicifolia*, and *Chiliotrichium diffusum*. The first two species are highly palatable to both sheep and guanacos. But the latter, an increaser on the range, is not palatable to sheep, but is eaten by guanacos. Overall, nirre was the most important browse species, both in terms of volume consumed, and frequency of occurence in the samples. Nirre is also the most abundant browse species due to its extensive occurence in the area, and low growth form. All three trees of the *Nothofagus* genus occuring on the study area were identified in the rumen samples.

The third most important component of the diet was the tree-born epiphytes, lichens, and fungi. The consumption of these plants paralleled that of the browse group, being high in the summer and low in the winter. The seasonal percentage in the diet varied little, from 8% to 14%. The most important species were the misteltoe, *Mesodendrum punctulatum*, and the lichens of the genus *Usnea*. All three of these types of forage were eaten as the guanaco browsed in the tree crown, and as windfall. The fungi were important only in the fall, at the end of their normal growth cycle, when they had fallen to the ground. Due to their extremely high digestibility and high water content, both the fungi and the lichens would tend to be underestimated in the analysis of the rumen contents and in fecal analysis.

Forbs were eaten throughout the year; however, they were important in the diet only in the spring months. This consumption reflects the greater abundance and availability in the spring. In general, the grasslands of Patagonia are not productive forb ranges. The only forb species important in the rumen samples was the common dandelion, *Taraxacum officinale*.

9.4.2 Diets of Sheep and Guanacos on Common Range

The comparison of annual and seasonal diets of sheep and guanacos was made on the basis of the analysis of fecal pellets collected from range lands used by both sheep and guanacos the year round. The specific range area studied was in the northeastern corner of the study area, of about 54,000 hectares (see Figures 1 and 47). This area supported the largest winter sheep herd of the estancia. In 1973 the area was stocked with 87,000 sheep at the beginning of the winter. The sheep were moved onto this winter range in late May, and were removed to spring range in mid November when new plant growth had begun on the spring range areas. Small herds of sheep used the area during the entire year, but the total numbers seldom exceeded 5,000 sheep except during the winter months.

The area was also the best remaining guanaco range on the island. Guanacos in the area were all resident, and highly territorial. Territories were generally near the forest patches, but also included the open grasslands. In the fall of 1973 this population numbered approximately 2,400 guanacos.

The fecal analysis technique was developed by Baumgartner and Martin (1939) to determine the food habits of squirrels. They discovered that the histological characteristics of fragments of plant epidermis were distinct for each species, even after digestion. The technique has been since used on many species of mammals and birds (Burrell 1977), and has proven useful in estimating monthly, seasonal, and annual diets (Hansen and Dearden 1975, Hansen and Reid 1975). Recent studies have also shown that with careful sample preparation and analysis, fragments of all plants eaten can be detected in feces (Burrell 1977, Hansen *et al.* 1973). Further, Todd and Hansen (1973) and Anthony and Smith (1974) have shown that the quantification of bighorn sheep and deer diets, respectively, by fecal and rumen analysis were similar. Dearden *et al.* (1975) found that fecal analysis of digested and simulated digested residues were not significantly different for reindeer, domestic cattle, and bison. Other studies (Hansen *et al.* 1973, Hansen and Reid 1975, Hansen and Clark 1977) have used fecal analysis to describe overlap in diets of ungulates of the North American range lands, and to analyze the effects of competition between domestic stock and wild cervids (Hubbard and Hansen 1976).

The diets of guanacos and sheep to a lesser extent, showed a considerable amount of seasonal variability (Table 31). This variation in food habits was undoubtedly a response not only to competition, but also to seasonal availability, plant phenology, and nutritional needs.

The food habits of the sheep were much more constant throughout the year than those of the guanaco. The major change in the sheep diet was the switch from grass to grass-likes in the spring (Figure 46). If we combine these two classes, there is little change in the diet. Grass and grass-likes made up 77.5% of the annual diet, and varied from a minimum of 67.9% in June to a maximum of 87.0% in April. The browse and forb consumption was quite constant throughout the year, and browse was little used (Table 32).

Even though the fecal fragments were not classified to species, qualitative notes of species composition of the diets were made. In general, the forbs, grasses, and grass-like species in the diets were the same in both diets. The actual plants eaten by the guanaco are listed in Table 33. However, while the grasses and forbs eaten were virtually identical in both herbivore diets, the browse species eaten were quite distinct. In several samples, notably the September sample, there was virtually

Table 31. Food habits of guanacos and sheep from parklands near Sec. Rio Grande, Isla Grande, Chile. The tabled values are mean percent of the diet ± the standard deviation.

GUANACO

Month	Grass	Browse	Forbs	Grass-like
February	31.9 ± 6.7	13.7 ± 2.8	7.5 ± 4.0	46.9 ± 9.2
April	55.1 ± 7.8	8.5 ± 5.0	11.2 ± 5.0	25.1 ± 7.1
June	7.9 ± 2.5	89.6 ± 2.9	2.2 ± 2.4	0.3 ± 0.6
September	40.9 ± 7.3	52.3 ± 8.4	4.9 ± 1.7	3.2 ± 3.4
October	56.5 ± 16.7	25.6 ± 10.9	9.0 ± 4.3	9.0 ± 3.0
December	36.6 ± 9.5	32.8 ± 8.8	8.4 ± 2.8	22.3 ± 9.3
Mean	38.1 ± 17.8	37.0 ± 30.0	7.2 ± 3.2	17.8 ± 17.4

SHEEP

Month	Grass	Browse	Forbs	Grass-like
February	46.2 ± 12.5	15.2 ± 6.7	7.2 ± 4.3	31.3 ± 10.3
April	50.1 ± 8.9	7.5 ± 5.6	5.4 ± 3.2	36.9 ± 12.0
June	58.2 ± 18.0	24.2 ± 11.5	7.6 ± 4.0	9.7 ± 5.1
September	50.3 ± 7.0	20.1 ± 5.2	8.3 ± 3.8	21.3 ± 4.8
October	16.9 ± 6.3	4.8 ± 1.4	9.0 ± 6.6	69.3 ± 13.3
December	42.0 ± 9.6	23.7 ± 10.9	7.6 ± 5.4	26.7 ± 4.2
Mean	43.9 ± 14.3	15.9 ± 8.3	7.5 ± 1.2	32.5 ± 20.3

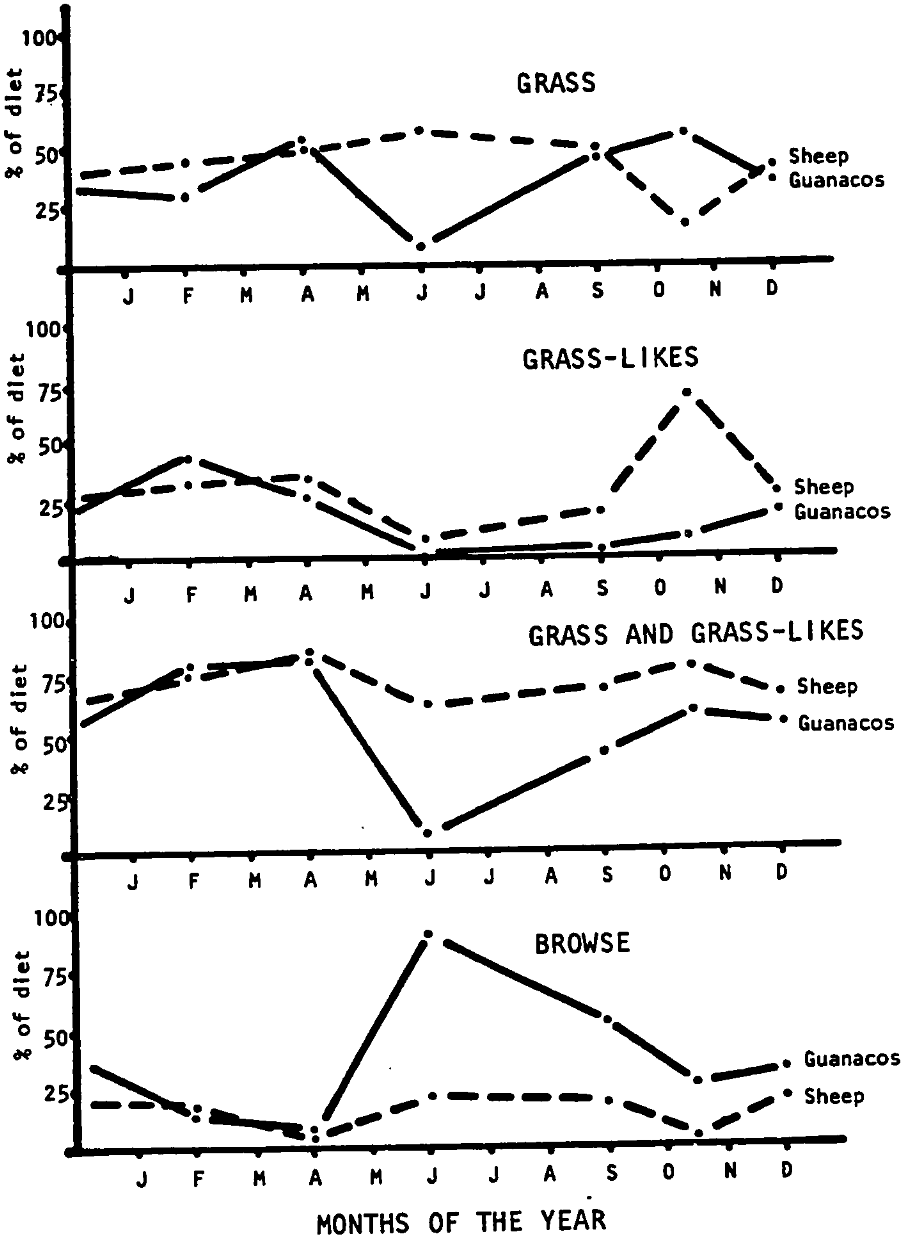

Figure 46. A comparison of the diets of sheep and guanacos from sympatric range. The data are based on the results of fecal analysis.

Table 32. Annual dietary preferences of sheep and guanacos. The preferences were calculated using the fecal anlysis data, based on the selectivity coefficient of Ivelev (1961).

		SHEEP		GUANACOS	
Forage Class	Availability	Diet	Ivlev's E	Diet	Ivlev's E
Grass	45	46.2	+0.013	38.1	-0.085
Grass-like	15	31.3	+0.352	17.8	+0.085
Browse	30	15.2	-0.327	37.0	+0.104
Forbs	5	7.2	+0.180	7.2	+0.180

no overlap in the browse species eaten. The guanacos ate the beech tree species (lenga and nirre) almost exclusively, while the sheep ate the lower growing shrubs. The winter diet of the guanaco also included the mistletoe, lichens, and fungi that were available to the sheep only as wind-fall, whereas the guanaco with their long legs and necks could browse directly.

9.4.3 Dietary Overlap in Sheep and Guanacos

The overlap in the diets of guanacos and sheep occupying common range was calculated using Kulcyznski's formula (Hansen and Reid 1975), based on the data from the fecal analysis presented above. The similarity index (SI) represents the percentage of the two diets which are identical, and is calculated as:

$$SI(jk) = 100(2\sum \min(Pij, Pik)/\sum(Pij + Pik)) \quad (12)$$

where Pij and Pik are the percentages in the diets for the food "i" in the two species diets "j" and "k" that are being compared.

The results of the calculations show that the overlap is greatest in the summer and lowest in the winter (Table 30). The average overlap for the entire year is 67.7%.

The validity of calculating dietary overlap on the basis of forage class data, rather tnat plant species data deserves comment. It is obvious that estimates of overlap based on forage class data would be an over-estimate of overlap if the species of plants within the forage classes eaten by the two herbivores were different. For example, Hubbard and Hansen (1976) calculated overlap between

Table 33. Diet similarity or overlap between guanacos and sheep by season, based on fecal analysis data.

Month	Similarity index	Standard deviation
February	76.6	±17.8
April	84.7	±11.7
June	32.0	±12.5
September	49.0	± 3.9
October	32.4	±13.6
December	80.4	± 7.5
Mean	67.7	±24.7

horses and cattle in the mountain shrub ecosystem to be 71% based on species level data. If we group the plant species listed in each of the diets into forage classes, and recalculated the overlap, we get 91.0% overlap. It is evident that grouping under these conditions will tend to mask real diet differences.

However, I feel that the calculations of overlap based on forage class data are useful for the following reasons. First, qualitative estimates of the species present in each of the different forage classes were made, with the result that the grass, grass-like, and forb species in the diets were found to be nearly identical.

These were the major components of the total diet. Second, the plant species identified in the guanaco rumen samples, listed in Table 30, were also those considered by sheep experts to be the primary foods of the sheep on the study area (Edwardo Tafra, per. comm.). Third, analysis of exclosure data showed that up to 95% of the annual forage biomass is removed each year from the grassland ranges. Only the browse is not fully utilized. Thus, overlap may be minimal early in the growing season, when there is a full complement of plants from which to choose, but as the forage is depleted, the choices are reduced, and only a few species of forage are left. Hence, in these times of limited forage, random probabilities predict that the species of plants eaten would be overlapping.

Furthermore, an analysis of dietary overlap based on plant species data are likewise not always applicable. Lamprey (1963) and Hansen and Ueckert (1970) found that different herbivores may eat the same plant species, but eat different plant parts; the herbivores were found to specialize on stems, leaves, shoots, fruits, and seedheads. Analysis of overlap, purely on the basis of plant species, and not on plant parts, would result in an over estimation of overlap.

A second concern is whether comparisons between herbivores with different digestive systems, and plants with different digestibilities are valid. It has been suggested that correction factors are needed to account for these differences. However, Hansen et al. (1973) on the basis of their work with deer, elk, antelope, sheep, cattle, and horses, felt that correction factors were not required to account for these differences between herbivores and plants. They felt that if care was taken in sample preparation and analysis, the results would reliably reflect actual diets.

9.5 The Impact of Guanaco-Sheep Interactions

The results of the previous sections on habitat use and food habits of guanacos and sheep indicate that there is a considerable amount of niche overlap between the guanaco and domestic sheep. Furthermore, the invasion of domestic sheep has dramatically changed the niche and therefore the abundance of the guanaco throughout much of its former range. In this section, I will evaluate the extent of the changes in the niche of the guanaco resulting from interaction with sheep, and examine how guanacos and sheep have partitioned the resources of the environment, thus allowing coexistence in certain parts of their ranges.

9.5.1 Guanaco Habitat Use Changes

The habitat niche of the domestic sheep is entirely included within the habitat niche of the guanaco, and sheep grazing has apparently eliminated the guanaco from much of its former range (see Figure 17). In Figure 47 the idealized relative densities of the current guanaco and sheep populations are plotted along the macro-habitat ecocline, based on the results of the previous sections. The figure shows that the sheep, with their more restricted habitat preference have supplanted the guanacos in the center of their former habitat (see Figure 43), and are sympatric with the guanacos at the fringes of their own range. In the extreme edges, the deserts and the closed forest communities, the sheep have not become established, and the guanacos exist alone at low population densities.

Circumstantial evidence suggests that competition with introduced sheep for the range forage was the ultimate factor causing the exclusion of the guanaco from much of its former range. First, the decline in guanaco

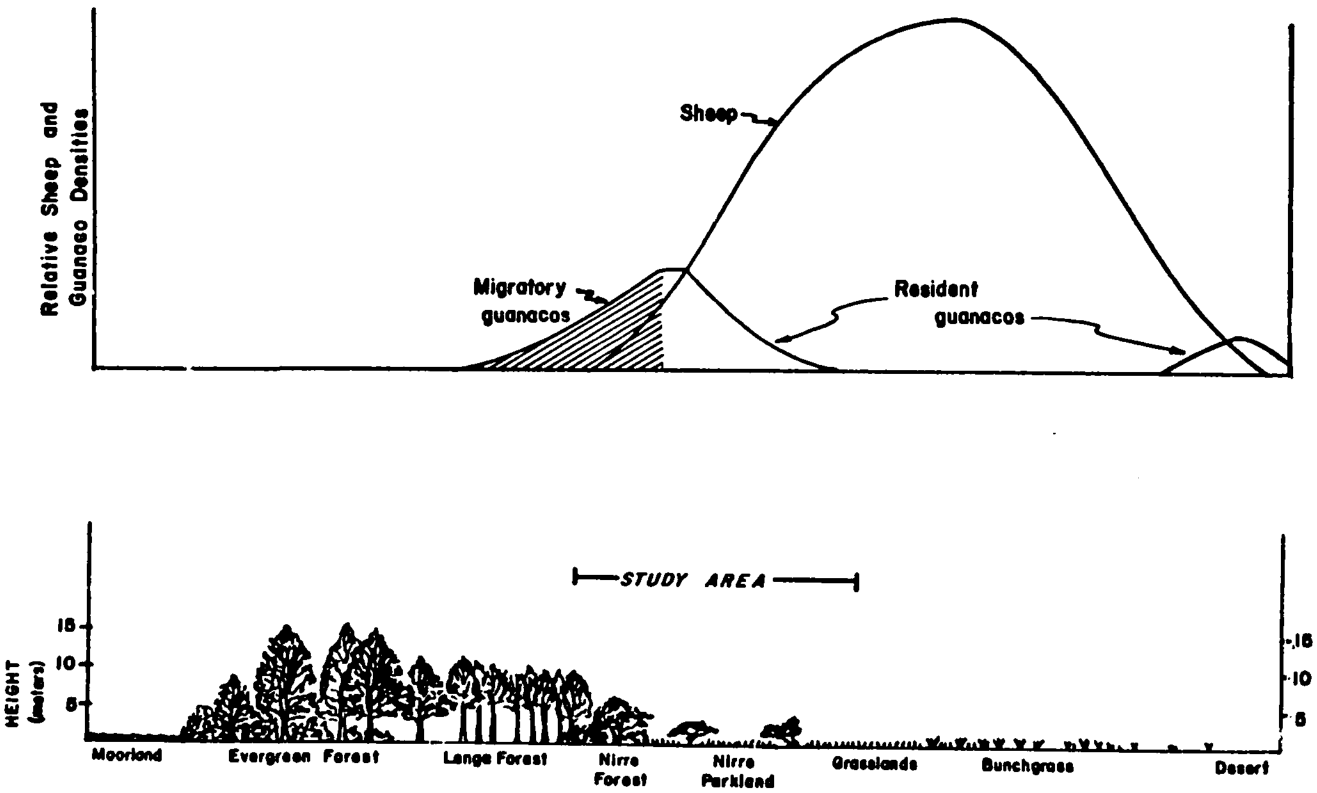

Figure 47. The relative densities of guanacos and sheep along the habitat ecocline of southern Patagonia.

numbers is highly correlated with the increase in sheep numbers; the Spearman rank correlation coefficient is -0.87 and is significant at the P=0.05 level (see Table 3 and Figure 34 for the actual data).

Second, guanacos have successfully repopulated areas where sheep have been removed. Rottman (per. comm.) reported an annual guanaco population increase of approximately 10% for guanacos repopulating former sheep range in an area that had been annexed to a national park. Sheppard (1971), Pianka (1974), and Krebs (1978) stated that the expansion of one species population subsequent to the removal of its competitior is the best evidence for competitive exclusion. Pianka (1976) called this phenomenon "ecological release".

Third, within the province, there are areas that are prime sheep range, but due to natural hazards, these areas have not been stocked with sheep. In these areas, guanaco populations often thrive. The best example is the guanaco population within the area fenced off around the Pali-Aike lava beds in the northeast sector of the province. Within this small area of less than 75 square kilometers, 500 guanacos were censused in 1975 (Raedeke 1978).

Direct evidence of competive exclusion of guanacos by sheep comes from the observation of habitat shifts with seasonal increases in sheep numbers on the study area. Guanacos shifted from heavily utilizing the open grasslands when sheep were not present to greater use of the forest patches when sheep were present in large numbers. This was observed both on summer and winter ranges.

This later observation of seasonal habitat shifts makes it appear that competitive exclusion was caused by interference competition. However, sheep are not physically or behaviorally dominant over guanacos, and did not displace guanacos through social interactions, since it was common to observe sheep and guanacos grazing interspersed on the grasslands without conflict. Instead, the movement of sheepherders and their dogs tending the sheep appeared to displace the guanacos for a period of time. Be this as it may, even if guanacos were not displaced by sheep and the herders due to interference, the guanacos would eventually be displaced by the depletion of the forage resource due to sheep grazing (i.e. exploitation competition). The typical heavy grazing pressures of sheep on the ranges in Magallanes reduces the carrying capacity of the ranges for guanacos through nearly compete seasonal depletion of the forage. Hence, guanacos that had been displaced by sheep would face a greatly reduced survival due to a reduction if forage if they returned to their former range after the sheep had been removed. Thus competition by exploitation of the forage resource by sheep appears to be the ultimate cause of some shifts in guanaco habitat use.

9.5.2 Guanaco Food Niche Shifts

The study of the diets of guanacos and sheep reveals a considerable amount of overlap in food preferences between the two herbivores, and a shift in the diet of the guanaco when interacting with sheep.

The dietary shifts of the guanaco support the hypothesis that the interaction of sheep and guanacos is a competitive interaction. The diet of the guanaco shows a distinct shift with an increase in interspecific competition. In the summer when potential competitive pressures are low, due to abundant forage, and low sheep densities, there was broad overlap in the diets of sheep and guanacos (see Table 33 and Figure 50). However, in the winter, when sheep numbers had increased over 10 fold, and the forage availability was reduced, there was a significant reduction in dietary overlap. Under these circumstances, the guanaco shifted from grass and grass-likes to browse. The shift is not simply a seasonal phenomenon, related to nurtitional value of browse or seasonal preferences, since the shift did not occur in guanaco diets on winter ranges without interacting sheep (see Table 29, samples G15, G16, G17, G1, G2, and G4).

Furthermore, the breadth or diversity of the guanaco diet declined sharply with the onset of competition with sheep. The diet was restricted to a smaller number of forage items in the winter during intensive competion with sheep. Again, the guanacos on ranges without sheep did not show a reduction in the diversity of items in the diet (see Table 29 and 31, and Figure 50).

The data further indicate that the shift in the forage niche of the guanaco, due to interaction with sheep, can occur at any time of the year. From the analysis of two guanaco rumen samples from sheep summer range (samples G7 and G23, Table 29), it appears that these guanacos shift their diet with summer comptition with sheep. In both samples, the overlap with the summer diets of sheep was low, and the diversity of the diets was also low. Although these results are tentative, since the sample size is small, it looks as though the guanacos and sheep ate largely different foods when on common range, and identical foods when on separate ranges.

Apparently the shift in the diet of the guanaco was initially caused by interference competition with sheep. This conclusion is based on the dramatic shift in the guanaco diet from grass to browse immediately following the introduction of sheep onto the range in late May (see Figure 44). The effects of interference competition would be noted immediately since it depends only on the number of competing individuals. Exploitation competition depends on the depletion of the forage resource, and hence, could not occur instantaneously. The hypothesis of initial interference competition is further supported by the observed gradual increase in the grass component of the guanaco diet, counter to the decline in abundance of grass on the range; possibly as the guanacos become accustomed to the presence of sheep and herders on the range. However, exploitation competition must also be an important mechanism, since the dietary overlap again decreases in the early spring, with the bloom of new plants, while sheep are still abundant on the range.

While both herbivore species would be inhibited by the overlap in forage use by the other species, there is strong evidence to support the hypothesis that interspecific competition affects the guanaco to a greater extent than it does the sheep. First, the sheep diet was relatively constant throughout the year, regardless of the presence or absence of guanacos. A test for seasonal changes in the sheep diet based on the forage classes of grass and grass-likes, browse and forbs, shows no significant seasonal changes (ANOVA, with P=0.05). The seasonal changes that are observed (i.e. the slight increase in browse consumption in the winter) was typical of the sheep diets on most ranges in Magallanes in general, and was most likely the result of intraspecific competition for the reduced range forage.

Further, the diversity of the sheep diet showed no obvious change during the period of most intensive competition. The minor changes that were observed apparently resulted from changes in seasonal forage preferences, or again, intraspecific competition.

9.5.3 Coexistence of Guanacos and Sheep

Competition is widely accepted as a major force underlying the different ways in which species present in the same community utilize resources. Competition promotes the use of different resources, and generates ecological diversity (see Schoener 1971 for a review).

The relationship of guanacos and sheep approximates the "included niche" model of interspecific competition proposed by Hutchinson (1957), with the qualification that the fundamental niches of both species are reduced by competition. The sheep, with the more specialized niche, have excluded the guanaco from much of their former range. The two species apparently coexist due to niche shifts by the guanaco where alternate habitat and forage resources exist.

The success of the guanaco in its current or realized niche can be attributed to the complexity of the habitat, and the ability of the guanaco to utilize alternate forage. Habitat complexity alone has been shown to allow coexistence, both in mathematical models (Horn and MacArthur 1972) and in the laboratory (Gause 1934, Huffaker 1966). The complexity of the habitat contributes to the survival of the guanaco in two ways. First, the structural complexity of the habitat (i.e. the interspersion of pampa and forest) provides a refuge from human harassment. Second, during periods of intensive interspecific competition, the forests provide an alternate and exclusive forage for the guanacos. This exclusive resource consists of any palatable forage over 75 cm above the forest floor. The guanaco food habits data clearly show a shift toward browse during competition. Undoubtedly, the forage resource of the forest is more important than the refuge, since the lenga forest, lacking in forage, does not provide suitable alternate habitat in times of intensive competition.

9.6 Seasonal Range Use and Competition

In the analysis of competition in the previous sections, the temporal dimension of the niche was not fully considered. Theoretically, it is possible for potentially competing species to partition the resources of an environment on a temporal basis: first, if the limited resource is continually renewed, and use at one time does not reduce future resource abundance; or second, if competition occurs only through interference, so that resource use during different time intervals obviates actual contact between the species. This is asserted to be quite rare in natural systems as a whole (Schoener 1974b), although not uncommon among ungulates.

In the case of guanacos and sheep, the limiting resource is evidently forage. Use of the forage at different times of the day or seasons of the year is unlikely to reduce competition since the forage resource is produced in a restricted season of the year, and competition is ultimately through joint use (exploitation competition). However, seasonal use can determine which herbivore is adversely impacted and the degree of the impact. For instance, if two species use the same area, but one in summer and the second in the winter, only the second species will be affected.

In this section, I will describe the competitive relationships between sheep and guanaco as affected by season of use. The study area can be divided into five types of sheep-guanaco seasonal use patterns: winter-winter, summer-yearlong, summer-winter, spring-yearlong, and winter-yearlong (sheep use listed first, guanaco second). The distribution of these range types is given in Figure 48.

9.6.1 Winter-Winter Range Use

Winter range of the migratory guanacos overlaps with sheep winter range along the shores of Useless Bay, and to the north of Lago Blanco. These are currently critical areas for guanacos, since these sheep winter ranges are overstocked. In severe winters, when snow becomes crusted and covers the low vegetation, all the livestock and guanacos are concentrated in the last patches of forage,

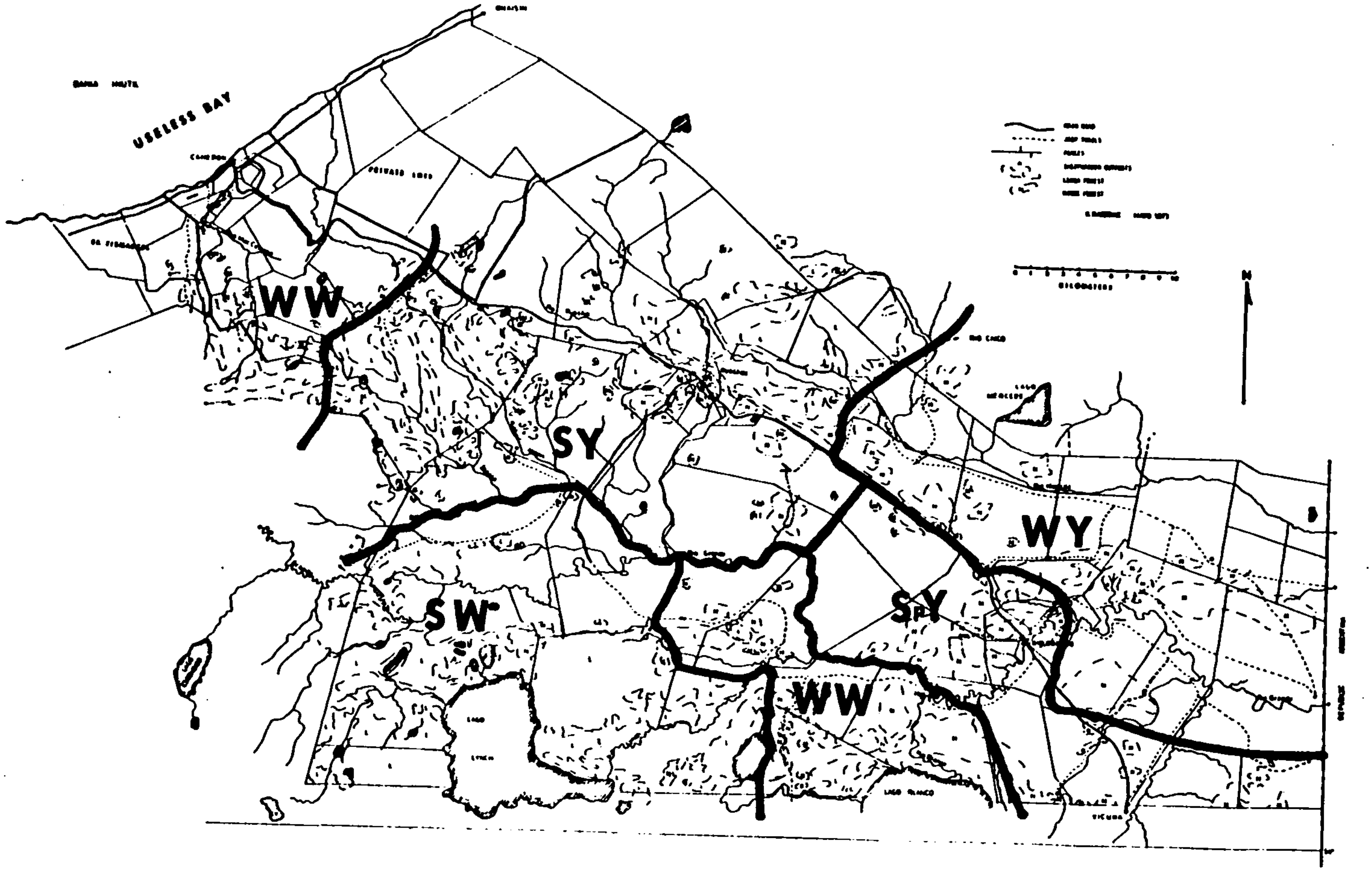

Figure 48. Seasonal range use by sheep and guanacos on the study area. The first letter is the season of use by sheep, and the second is the season of use by guanacos.

and large die offs of both species occur. In 1973 up to 50% of the guanacos and 35 to 45% of the sheep on these ranges died. However, this situation may be corrected in the future, since it is clearly recognized that these ranges are overstocked with sheep, and sheep numbers are being reudced (C. Bristillo, per. comm.).

9.6.2 Summer-Winter Range Use

Summer use by sheep and winter use by migratory guanacos results in "unilateral competition" or amensalism, where only the guanacos are impacted by competition. This type of range use is found in the southwest corner of the estancia, just north of the continuous forest. The wintering guanaco population in this area has the highest density of any guanaco population within the island, and probably in all of South America. Since the sheep industry on the island, and the province in general, is currently limited by sufficient winter range, the summer ranges are not overstocked. The forage in these summer range areas is not fully utilized as on the winter range. This range area has a stable trend, and is in fair to good condition. In most years there is adequate winter forage for the guanacos. However little is known about the ecology of these guanacos, since they are inaccessible the year round.

9.6.3 Summer-Yearlong Range Use

This type of common range use is found in the north central section of the study area. Since the summering sheep herds are limited by the amount of winter range available, the summer of the study area. Again, these summer ranges are not overstocked with sheep, and the general range condition is fair, with a stable trend. However, the productivity of this area is quite low. Guanacos in the area are able to maintain their predominantly grass diet throughout the year, and winter survival is average. In the winter of 1973, the mortality was only slightly higher than average. Due to the low quality of these ranges, the guanaco population is only moderate, with 1800 guanacos (roughly one per square kilometer), with most concentrated in the eastern portion, with few guanacos on the lateral moraine topography on the west.

9.6.4 Spring-Yearlong Range Use

This type of common range use is quite limited, and found only in the southeast corner of the estancia. The area is used as spring range for the ewes during the lambing season. The range condition is generally fair to good, as the area is somewhat protected for the lambing ewes. Competition pressure on the resident guanacos is thus moderate, and the guanacos do not seem to shift much from tneir year-round grass diet. Guanaco survival in this area is better than average, with only about 20% mortality in 1973. However, the total area in this classification is quite small, and contians only about 300 guanacos (2.5 per square kilometer).

9.6.5 Winter-Yearlong Range Use

The northeast corner of the estancia is the primary sheep winter range. The area supports 75% of the total winter sheep herd. The food habits and range use of the guanacos and sheep of this area were discussed in detail in the earlier sections, where it was indicated that strong competition exist between the two species. However, the area still supports the largest non-migratory guanaco population on the study area (2400 guanacos, or

4.0 per square kilometer). In general, these ranges are overstocked with sheep, and the range trend is downward. After the severe winter of 1973 the winter sheep population on the area was maintained by management at a level approximately 15% below the former population size. Range conditions should improve, but greater reductions are necessary to prevent a continued deterioration of the range. In a later section, I will attempt to model the competition dynamics between the sheep and guanacos in this area.

9.7 The Dynamics of Interspecific Competition

The results of the earlier sections clearly show that the guanaco and sheep of the study area compete, at least to some degree, for the finite resources of the environment. It was also shown that the guanaco has responded to severe competition with the sheep by niche shifts both in habitat and forage utilization where it has had an opportunity to do so; and a parallel reduction in overall distribution and population size has occured. However, these results alone do not indicate the stability of the competitive "equilibrium" that the populations may have reached. Nor do we yet have any predictions of the impact of competition on future guanaco populations. In this section, I will construct models of the dynamics of the interspecific competition, based on the information presented in the previous sections, and discuss the predictions provided by these models, with regards to future population size. I will also suggest how these models could be validated by future work.

Since competition theory readily lends itself to mathematical models, a considerable number of models and systems of models have been developed that deal with all aspects of competition theory. The purpose of this section is not to add to this to this already burgeoning array of models, but rather to examine the most promising of these, and test their predictions against the results of the earlier sections of the study. I will attempt no comprehensive review of the field; such a review is given by Hutchinson (1978).

Two classes of models seem worth examination: first, I will start with the simple forms of the Volterra equations, since they have been the basis of much of the current competition theory, and second, I I will examine some of the newer energy balance models that deal with the actual mechanisms of population growth and competition.

9.7.1 The Volterra Competition Model

Much of the theory of competition is based on the now "overworked" Volterra equations, which model the simultaneous growth of competing species as a set of differential equations of the form:

$$dN_1/dt = r_1N_1/K_1(K_1 - N_1 - A_{12}N_2) \qquad (13)$$

$$dN_2/dt = r_2N_2/K_2(K_2 - N_2 - A_{21}N_1) \qquad (14)$$

where the "r's" are the instantaneous rates of growth per individual for the two populations; the "K's" are the carrying capacities of the habitat for species "N1" and "N2". The competition coefficients are the "A's" (usually written as the Greek symbol alpha): A12 is the relative effect of species 2 on species 1, and A21 is the relative effect of species 1 on species 2. If there is no detrimental competitive effect, (i.e. the competition coefficients are both zero) then both populations grow logistically.

There are several difficulties inherent in the use of the Volterra equations. First, like the logistic equation, they are probably an oversimplification of the competitive process (see Gilpin and Ayala 1973, Schoener

1974a). Second, the alphas are difficult to compute, and may even mask the real mechanisms of the competitive interactions.

However, for the purpose of the present discussion, the Volterra equations are a logical starting point since they are mathematically tractable, the bahavior of the model is well known, and the growth of the sheep population since introduction is quite logistic-like.

To evaluate the dynamics and qualitative outcome of this model, we ask, what are the population levels at equilibrium (i.e. when the growth rate of both populations is zero)? The mathematical or graphical solutions to the model are given in most general ecology texts (see Wilson and Bossert 1971, Pianka 1974). There are four possible equilibrium solutions to these equations: a stable equilibrium with both species present at some population size; unstable equilibrium, where either species can ultimately displace the other species, depending only on the initial densities; and finally, the competitive exclusions of one species by the other. The solution of the equations shows that general results of the model can be determined by computing the competition coefficients and carrying capacities for both species.

the conditions for the equilibrium solutions are given in Table 34.

To evaluate the Volterra competition model for guanacos and sheep, the interactions of the two species in the northeastern section of the study area will be analyzed, based on the data presented in the previous section on food habits and habitat utilization.

The carrying capacities of the two populations were calculated from the 1972-1975 sheep population numbers. Since 80,000 sheep annually used the area for six months, the carrying capacity was calculated to be half, or 40,000 sheep. The carrying capacity for guanacos was estimated to be 13,000 based on body-equivalent weights (i.e. one guanaco equals three sheep).

Table 34. Summary of the four possible cases of competition under the Volterra competition equations.

	Conditions	Results
(a)	$A_{21} > K_2/K_1$ and $A_{12} < K_1/K_2$	Species 1 excludes 2
(b)	$A_{21} < K_2/K_1$ and $A_{12} > K_1/K_2$	Species 2 excludes 1
(c)	$A_{21} > K_2/K_1$ and $A_{12} < K_1/K_2$	Unstable equilibrium
(d)	$A_{21} < K_2/K_1$ and $A_{12} > K_1/K_2$	Stable coexistance

The competition coefficients were calculated on the basis of the resource utilization data, both for habitat and forage. The competition coefficient calculated is an overall "multidimentional" coefficient, which equals an appropriately weighted linear combination of the "one-dimensional" coefficients based on forage and habitat data (May 1975). The actual calculation procedures are given in Appendix B.

The results of this analysis, based on the competition coefficients and carrying capacities defined above, predict that the guanacos (species number 1) should be excluded from the habitat through competition with the sheep (species 2). When the "Aij's" are calculated on the basis of the annual average forage and habitat utilizations, we get the following parameter values:

$$A12 = 0.825 \text{ and } A21 = 1.164$$

$$K1/K2 = 0.33 \text{ and } <2/K1 = 3.0$$

which gives the relations defining the outcome of competition as follows:

$$A12>K1/K2 \text{ and } A21,K2/K1 \qquad (15,16)$$

which signifies that the sheep (N2) will out compete the guanacos for the limited food resources, and the guanacos will be eventually excluded from the range where they are now sympatric.

The same competitive relationships result when the parameters are calculated on the basis of the winter period, June through October, when the guanaco has shifted its forage niche in response to competition with sheep. The competition coefficients are: A12 equals 1.55, and A21 equals 1.03.

The overall conclusion from this model is that the guanaco will eventually be excluded from the habitat by sheep which appear to be competitively superior. There is little doubt that the sheep are competitively superior to the guanacos under the present management system. The sheep have been bred to be efficient converters of forage to animal biomass, and management attempts to maximize their utilization of the available forage resources through seasonal movements and herding. If we accept the Volterra model as an appropriate model for this system, we need to consider why the guanaco has not already been excluded from the area of range overlap.

The first possible conclusion might be that the model is appropriate, but the parameters were improperly estimated, leading to false conclusions. For example, if the competition coefficients were incorrect, it is possible that the model could have predicted stable coexistence of the two species. However, if we calculate the coefficients that would allow coexistence, the results show that the coefficients are different from the experimental results by a factor of two. Thus the results would seem to be at least qualitatively correct.

Second, since the Volterra model assumes that the environment is saturated, we might conclude that the guanaco population has persisted because management or predation has held the sheep numbers below the carrying capacity. Thus, if they were allowed to increase, the guanaco population would be excluded. However, this is unlikely, since we have seen in an earlier section that the sheep are near the long term maximum carrying capacity of the range, and may have even exceeded it, as indicated by the downward trend in stocking rates and range condition, high winter mortality and lamb loss.

Thirs, we might conclude that the Volterra model is inappropriate for this system, since several of the underlying assumptions are biologically unrealistic. The model depends on the following assumptions: 1) all inhibiting relationships between and within the populations are strictly linear, 2) all the values in the model are constant over time and in space, 3) the environment is completely homogeneous, i.e. all species use the same resources (Pianka 1974). However, we know that in real populations these assumptions are all violated to a certain degree. Parameter values and relationships, especially in temperate environments, change from individual to individual and with time and in space. Indeed, temporal variability in the environment alone may allow coexistence by continually changing the competitive relationships between the species. Furthermore, few ungulates live in homogeneous habitats; indeed, competition theory is based on the idea that natural selection will genetically fix divergent patterns of habitat utilization within heterogeneous environments, thus reducing interspecific competition.

On the basis of the results of the previous chapters, I would conclude that this last alternative is the most reasonable. The Volterra model does not appear to be appropriate for this system, and its predictions are not consistent with the results of the sections on population dynamics of sheep and guanacos. Furthermore, more complex versions of the same model are not likely to be of much use, since the underlying assumptions themselves seem to refute much of the competition theory that they purport to describe.

9.7.2 Energy-balance Models

Schoener (1974c) has developed a set of population growth models that are based on the partitioning of energy entering into the system both by individuals of a species, and also their competitors. These are mechanistic models, that is, they are based on the actual mechanisms of population growth, rather than the models like the Volterra model which statistically fit a descriptive model to the data.

The energy-balance model that is most appropriate for the guanaco and sheep populations are equations 5 and 3a of Schoener (1974c). The model consists of the following equations:

where species 1 is the guanaco, and species 2 is the sheep. The key to the symbols is given in Appendix C.

This system of equations models exploitative competition for overlapping resources with a fixed energy input. In the absence of competitors, both species would grow in a logistic-like manner, reaching some upper limit of population size, due to the fixed resources. In the given case, the sheep has its niche entirely included within the niche of the guanaco as we have seen in Figure 47. Thus all resources of the sheep are available to the guanaco. Furthermore, the guanaco has exclusive resources, such as the browse and tree-borne plants, that are out of the reach of sheep. These exclusive resources are represented as "I_{E1}" in the equations.

According to Schoener (1974c:272):

> "the species with the exclusive resource will obviously survive, but whether the other does or not depends on several parameters. Simple algebra shows that the two isoclines either (1) intersect once in the first quadrant, whence the singularity is a stable node or (2) fail to intersect, resulting in exclusion of the included species... In other words, for coexistence (1) the carrying capacity of the broad-niched species must be small; (2) the feeding efficiency of the included species must be large; (3) the likelihood of the included species getting an item of overlapping resource must be great; and (4) the death and maintenance rates of the included species must be small."

Considering the facts that the sheep are domestic animals, and artifical selection has selected for the exact characteristics given by Schoener for the included species, it would seem that the coexistence of both species in this system is assured. The graphic results of this model, as compared to the Volterra model are given in Figure 49.

In addition to coexistence, the model predicts that (a) the guanacos should persist at the present levels indefinitely unless the habitat is altered, (b) guanaco numbers will be insensitive to fluctuations in sheep densities (due to the non-linear nature of the phase plane isoclines), and (c) the numbers of guanacos that have survived are the maximum number that can exist on the exclusive resources and the limited shared resources available to the guanaco.

Several of the results of the earlier sections support the use and conclusions of this second model. First, the guanaco population dynamics results indicate that the population is indeed stable. An analysis of the population growth, based on a Leslie Matrix model (Leslie 1948) of the fecundity-survival matrix gives stability conditions, that is, the dominant eigenvalue is one, signifying a stationary population. Furthermore, indirect evidence presented in the earlier sections indicated that the guanaco population has not changed dramatically in the last decade.

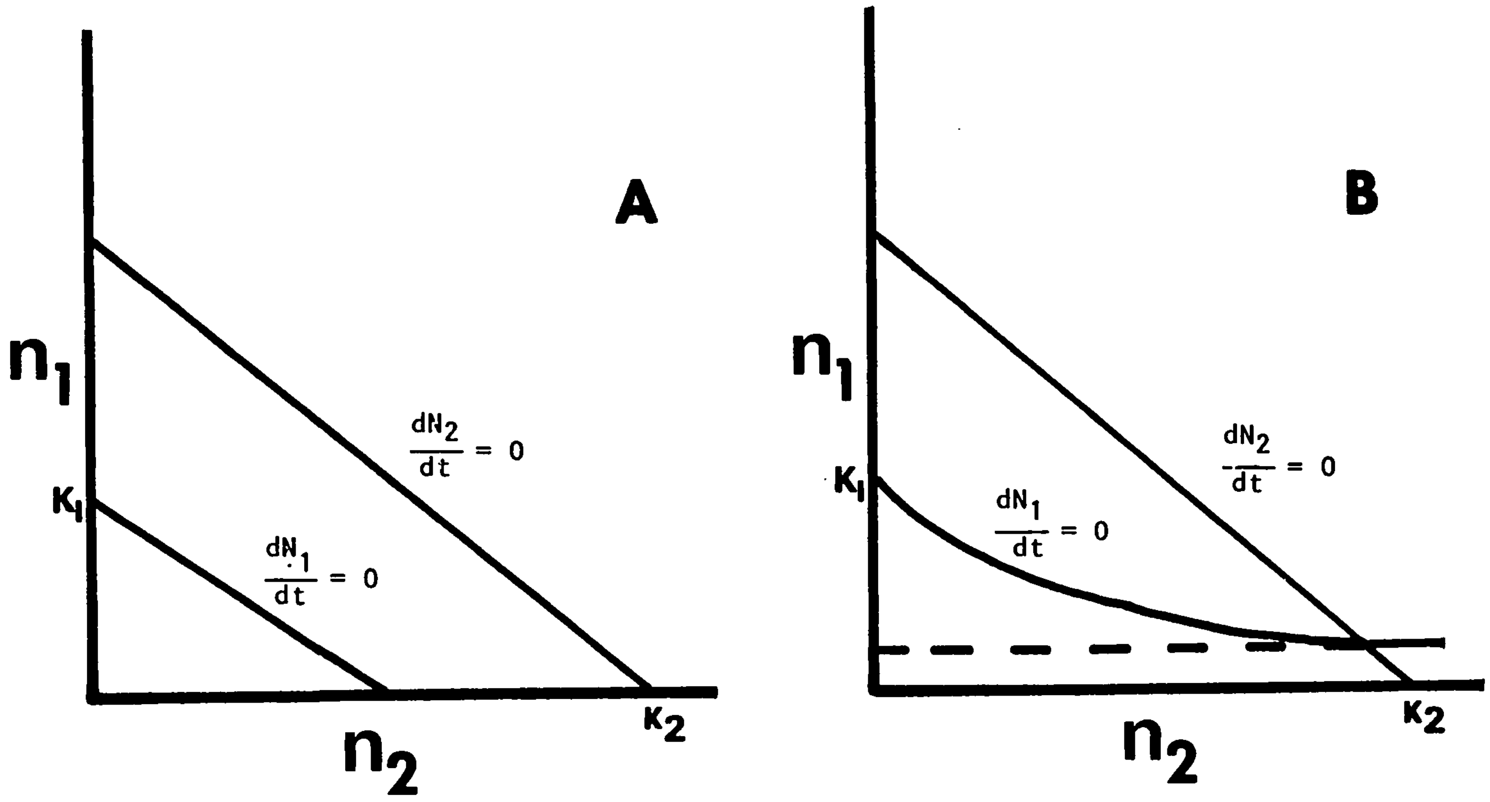

Figure 49. Graphic solutions to the competion models of Volterra (A), and Schoener (1974c) (B). In both cases, the guanaco is species 1, and the sheep is species 2.

Second, the 30% increase in the sheep herd from 1967 to 1973 did not noticeably affect the guanaco population numbers. The data from the present study further indicate that from 1971 to 1973 the guanaco population was stable.

Third, food habits data clearly suggest that the guanacos consume a large amount of forage that is excusively available to them in the critical winter periods. The upper limit on sheep browsing is about one meter, while the guanaco can browse as high as 2.6 meters. The browse above one meter is in a nearly unlimited supply, and contains a moderate amount of highly preferred plants such as the lichens, fungi, and epiphytes. This forage can undoubtedly sustain a guanaco, since several of the migratory populations in the continuous forest to the south of the study area, subsist where browse is the only winter forage available. These migratory guanacos exist where sheep cannot survive.

Fourth, in the severe winters when the grasses were crusted over with snow, mortality rates were lower in the guanaco than in sheep. In the winter of 1973, the sheep mortality in the interior ranges was close to 50%, or nearly five times the average rate. At the same time, guanaco mortality on the same ranges was not even double the average rate. Guanacos did not perish since the exclusive resource was virtually unaffected by the snow conditions that covered the grasses.

9.7.3 Validation of Competition Models

There are several ways in which either of these models could be validated. First, one could continue to monitor the population sizes of both species over time. The important parameters to consider would be the relative densities of the two species in the various habitats and changes in population density of one species relative to the other species.

Second, a more active research porgram could attempt to again evaluate the competitive relationships of the species periodically over time. This approach would be most appropriate if there were substantial changes in the habitats of the species, or in the management of the habitats or even the species themselves.

Third, since the guanacos apparently depend on certain seasonal foods, and the continued production of these foods in adequate amounts is necessary for their survival, one could measure the response of the guanaco population to changes in this food supply over time. For example, a continual reduction in the forest browse and the other tree-borne foods should result in a reduction of the guanaco population if the conclusions of the latter model are correct.

9.7.4 Predictions of Future Guanaco Population Trends

The prediction of the future trends in the guanaco population are directly dependent on the model that is selected as being the most appropriate for the system. The differences between the two models are dramatic, as the first model of Volterra predicts ultimate extinction, while the model of Schoener predicts persistence of the guanaco population at the present levels, even if sheep were to increase.

In the discussion of the two models, I concluded that the latter model was most appropriate. Even though this model predicts persistence of the guanaco, this conclusion is based on a static environment. Extinction is still possible if the environment changes as a result of habitat manipulation by man or by natural causes. For example, if the forest patches which provide the exclusive forage resource for the guanaco were substantially reduced, we would expect a reduction in guanaco numbers. Changes in the land use, such as heavier sheep stocking could also reduce the guanaco population, especially in the areas currently used by the guanaco in the winter, and sheep in the summer.

Furthermore, these models are both deterministic, and do not allow for changes in the environment, such as catastrophic winters, or disease under stress of poor range. Any stochastic variation in the parameters of the models would give a certain probability of extinction. This probability of extinction would be minimal in a large population, however, in a population already reduced to such low levels as the guanacos, this probability could be significant.

9.8 Theoretical Considerations of Niche Shifts

A substantial body of theory has been developed that deals with the manner in which animals partition the resources of the environment. Optimal foraging theory is a subset of this theory, and predicts the sort of niche shifts that are most likely to occur with a change in resources abundance due to competition (Pianka 1976). Optimal foraging theory is based on the premise that an animal will harvest its food in a manner that will maximize its Darwinian fitness (MacArthur and Pianka 1966). Recent reviews of the theory are given by Schoener (1971), Pyke *et al.* (1977), and Krebs (1978). In this section we shall see if the qualitative predictions of optimal foraging correspond with the observed changes in foraging patterns of guanacos and sheep.

9.8.1 Optimal Foraging Theory and General Predictions

Optimal foraging theory is based on contingency feeding models in which an animal "...weighs the per-unit energy gain form an item of food if caught and eaten against the expected gain if that item is skipped and only better items are searched for and consumed" (Schoener 1974a:4169). These models can be generalized to include decisions on habitat patches included in the itinerary of the organism by changing the parameter definitions. These results have been derived independently by no fewer than eight authors (Pyke *et al.* 1977), and have lead to the following three generalizations:

1. A reduction in food abundance should lead to an expansion of the diet, and possibly a contraction in habitat (MacArthur and Pianka 1966).
2. Whether a food item is included in the diet depends only on the abundance of better items (Schoener 1974b).

3. a prey type should be eaten on every encounter or never eaten (for fixed densities) (Pulliam 1974).

In these models, foragers are grouped into two types of feeders: those that have a fixed energy requirement and a limited amount of time to forage, with fitness increasing with time spent in other activities, the animal will need to maximize the net energy intake while it forages (called the "time minimizers" by Schoener 1971); and second, those that have a fixed amount of time to forage (or process the forage in the gut in the case of ruminants), but whose fitness increases with increases in energy obtained, should maximize the amount of energy obtained in the fixed foraging period (called "energy maximizers" by Schoener 1971). In both cases the net rate of energy intake while foraging will be maximized, and the three predictions given above are identical for both classes of foragers.

While many of the predictions of optimal foraging theory are yet untested, a number of studies have shown that animals do tend to forage according to the predictions of the models. Krebs (1978) has reviewed the results of these tests of the theory. In general, the best results are obtained from animals such as carnivores whose foods vary in capture and search costs, and caloric yield per item, but not in nutritional content. However, Belovsky (1978) concluded from his studies that the observed diet of the moose agrees with the predicted diets, which were based on the energy maximization hypothesis of optimal foraging theory. He generated his predicted diets using linear programming, with nutritional and thermoregulatory constraints.

Nontheless, many authors have commented that generalist herbivores are subject to several constraints that are difficult to reconcile with the basic assumptions of optimal foraging theory. First, unlike carnivores, the herbivore faces a changing optimal diet due to changes in the properties of its food, which often can not be detected until consumed (Krebs 1978). This, coupled with a long-delay learning mechanism (Westoby 1974) necessitates a continual sampling of the different food types to monitor the changes in nutritional value of the foods. Westoby (1974) predicted that the optimal diet of range sheep should consist of only one or two plant species, based on the nutritional needs of the sheep, and a knowledge of the chemical composition of the plants. However, the observed diets of the sheep were much more diverse, and he concluded that the differences were due to sampling.

Second, it is impossible for a generalist herbivore to qualitatively rank each food item in the diet since the items are not independent of other foods taken in the same foraging period. Unlike carnivores whose different foods all provide the same relative mix of necessary nutrients, the foods of herbivores vary greatly in nutritional value. Hence the herbivore must eat a mix of different foods to provide the important nutrients or lack of "negative nutrients" such as secondary plant toxins (Westoby 1974). Freeland and Janzen (1974) argued that the concentrations of plant toxins in otherwise valuable foods is the main source of diet diversity and partial preferences in mammalian herbivores.

While the simplest contingency feeding models may not be entirely appropriate, Schoener (1971) argued that the nutritional constraints, and other factors mentioned, will be relatively unimportant, and the predictions of optimal foraging theory will still be valid. This is partially supported by the work of Belovsky (1978), Pulliam (1975), and Pyke *et al.* (1977).

9.8.2 Specific Predictions of Guanaco Foraging Patterns

On the basis of contingency feeding models and our knowledge of sheep foraging patterns, it is possible to predict how the guanaco niche should change with a decrease in forage abundance as a result of competion with sheep. To make thse predictions we need to assume first, that the guanaco, like most ungulates, is an "energy maximizer" second, that the net rate of energy intake per unit feeding time is the most important factor in the diet selection. Two types of resources will be considered, both food and habitat.

OPTIMAL DIET. A competitor can reduce the availability of a food item, but can not reduce its energetic or nutritional value. Thus, an item worth eating before the pressures of competition is worth eating with increased competition and reduced forage abundance (MacArthur and Pianka 1966). However, if the density of the highest ranked item is reduced, the diet should expand to include other items of lower rank. Selectivity should decrease as the chance of finding something better after skipping an item decreases. We would therefore predict that diet diversity would increase with an increase in competition. This increase in diversity should also increase dietary overlap between the competitors.

OPTIMAL HABITAT. A specialized competitor, one with distinct habitat preference like the sheep, can preferentiallly deplete some patch types to the extent that the forage value within those patches is reduced. The reduction can decrease the overall selectivity, and reduce the range of patches occupied, if the favorable habitat is limited. Thus, other, lower ranking patches can be added to the itinerary. In the case of the guanaco, the preferred habitat was preferentially depleted by the sheep. Hence, we would predict that with depletion, the guanaco should include other patches, such as the forest, in its itinerary.

Furthermore, if the patches contain different food items, a restriction in patches in the itinerary could reduce food niche breadth as well. Hence, with a somewhat specialized competitor, the original species in the habitat could become more a of diet specialist, contrary to the first prediction.

9.8.3 Comparison of Observed and Predicted Foraging Patterns

When we compare the observed and predicted niche shifts, several interesting patterns emerge that were not fully predicted by optimal foraging theory. The observed shifts in the habitat niche of the guanaco were described in an earlier section, and the food niche shifts are summarized in Figure 50. The breadth of the food niche was mesured by the trophic diversity index. A high trophic diversity index indicates a diverse diet

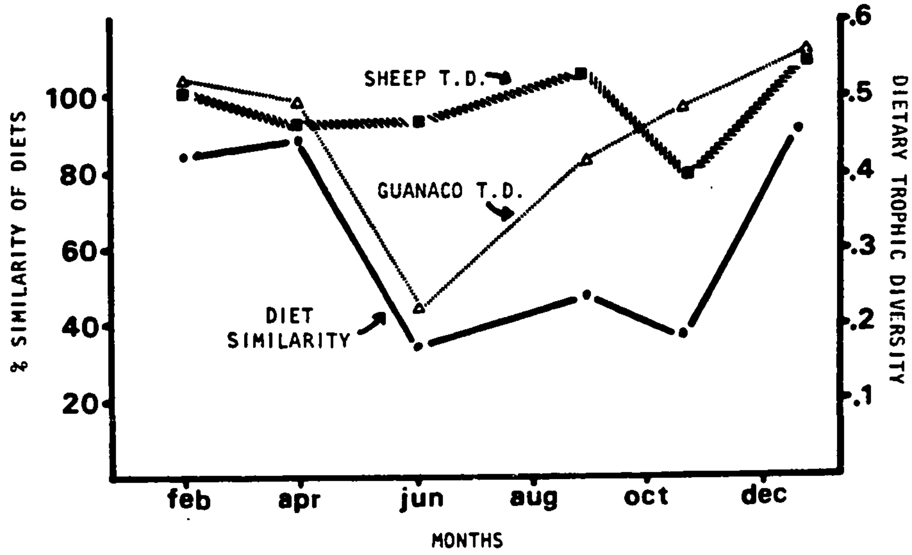

Figure 50. Dietary overlap between the sheep and guanacos, and trophic diversity (T.D.), by season on sympatric range.

(Hurturbia 1973). Shannon's (1948) formula was used to calculate the trophic diversity, based on the number of different plant types in the diet. In this analysis, the maximum index value possible is 0.602, representing the highest possible dietary diversity.

The results show that the winter diet of the guanaco, during the period of most intense competition has expanded, and includes more items than the pre-competition diet. However, the proportion of the items in the diet has changed dramatically, to the extent that the guanaco is now a diet specialist, as indicated by the reduction in trophic diversity of the diet from 0.491 in April to 0.214 in June. This decline in diversity of the diet is significant (P=0.05, based on ANOVA). This contraction in the diet resulted from a reduction in the types of habitat patches occupied. The guanaco shifted from a grazer on the grasslands to a browser and grazer in the forest patches. Without competition with sheep and preferential depletion of the grasslands, this change did not occur (see Table 32). With depletion of the grasslands by the sheep, the foraging value of the pampa for guanacos decreased to a value lower than that of the forest patches.

However, the predicted contraction in habitat patches should have been gradual, coinciding with the gradual depletion of the patches by sheep. But this was not the case. The guanacos contracted their habitat patches and expanded their diet before the sheep could possibly have depleted the grassland patches. Undoubtedly, there is an additional "cost of social interactions" with sheep that must be included in the energy balance equation of the simple contingency models. This would be consistent with the earlier observations of of interference competition of guanaco and sheep.

For example, in Schoener's (1974a) model of contingency feeding, the net enegy gained by the consumer is defined defined as:

$$\sum PiEi - CsTs \qquad (19)$$

where "..."Ei" is the net energy (potential minu pursuit and handling-swallowing costs) for a single item of Type "i"; Pi is the frequency of Type "i" in the environment (availability); "Ti" is the mean search time per item of available food; and "Cs" is the cost per unit serach time time" (schoener 1974a:4169). If a cost term for social interaction were added to this summation, then high costs of social interaction within some patches would reduce the foraging value of the patch and it would be dropped from the itinerary. This could occur even if the patch had not been depleted.

The foraging niche of the sheep, unaffected by social interactions to a large degree, shifts in accord with the predictions of optimal foraging theory. First, the diet of the sheep expands throughout the winter, as the grass is depleted. The dietary breadth also expands throughout the winter as grass availability decreases. In the spring, with the new growth of grass, the diet again contracts.

With the depletion of the grasslands, the sheep also show a shift in habitat. As the winter progresses, the sheep gradually start to use other habitat patches, such as the forest, the bogs, and the rush meadows. The shift into the forest by the sheep is not as dramatic as for the guanaco, since the forest has a low foraging value for the sheep, due to the short verticle reach of the sheep. This, coupled with a low nutritional rank for the browse, makes the forest a low ranking habitat for sheep. They can maximize their energy intake by including poor quality, but readily available grass-likes that were not selected earlier in the winter. The consumption of grass-likes by sheep increases dramatically during the late winter, until the new grass growth in spring (see Table 31).

The first prediction of optimal foraging models says that with reduced forage availability, the diets should expand. This was observed, however, the converse should also be true; that is, with an increase in forage availability, the diets should specialize. While the range of items in the diet does decrease, the diets do not specialize. The trophic diversity in both cases is near the maximum throughout the summer period. While we can only speculate, this diversity of the diet could be due to the nature of the forage and the nutrient needs of ruminants, which may only be met from a mix of forage items in the diet.

Clearly the predictions of optimal foraging theory, based on the proper contingency model can grealty aid in the understanding of habitat needs and the effects of exploitation competition on ungulates. However, without a detailed knowledge of the behavior of both species in social interactions, optimal foraging theory is unlikely to be an accurate predictor of foraging patterns.

CHAPTER 10

Conclusions

The hypothesis of the present study is that the growth of both sheep and guanaco populations of the study area is ultimately limited by the forage resource. Intraspecific and interspecific competition for the forage are the mechanisms that function to regulate both populations. Further, as a result of competition with sheep, the distribution and abundance of the guanaco population have been reduced.

Alternate hypotheses are that the guanaco population is limited by natural predators, harvesting by humans (hunting), introduced diseases, changes in the abiotic components of the environment (weather), and socio-physiological self-regulation.

The results of the present study clearly show that the sheep and guanaco populations are limited by the amount and quality of available forage. Both populations respond to a decrease in available forage by an increase in mortality and a decrease in natality. In the guanaco population, starvation accounted for 80% of the total mortality, and is clearly the dominant mortality factor. Other mortality factors, such as disease, hunting, and predation act in a compensatory fashion, and remove individuals from the population that would otherwise die of starvation. In the case of the sheep population, the long term records documented the decline of the population growth as the carrying capacity of the habitat was approached, the decline in the population size as the forage production declined due to overgrazing, and the subsequent increase in the population with an increase in forage production resulting from range improvements. Furthermore, starvation losses increased when the harvest rate was reduced, thus preventing an increase in the population size.

During the study period, competition for the available forage resources operated to limit the guanaco population in two ways. First, guanacos and sheep occupied the same habitats and were in direct competition for the forage. Intraspecific competition with the sheep inhibited the guanaco population through a depletiion of the forage, and by excluding the guanaco from the forage through social interactions (disturbance). In areas where sheep consumed nearly all the available forage, and alternate forage resources were not available to the guanaco, the guanacos were eventually displaced. Second, intraspecific competition operated to limit the guanaco population to the approximate level that could be supported by the resources that were available to the guanaco after competition with sheep. Territoriality in guanacos has evolved as a result of intraspecific competition for resources through natural selection at the individual level, and not as a means of population regulation. Interspecific competition sets the upper bound on the guanaco population size, and intraspecific competition maintains the population at or near this upper bound.

A model of the interactions of guanacos, sheep, humans, and the environment is given in Figure 51, represented by a flow diagram in formal System Dynamics notation. In this model, the species population size is determined by the difference between the birth and death rates. The forage supply available to the herbivores is determined by the difference between the rate of net primary productivity (NPP), and consumption and

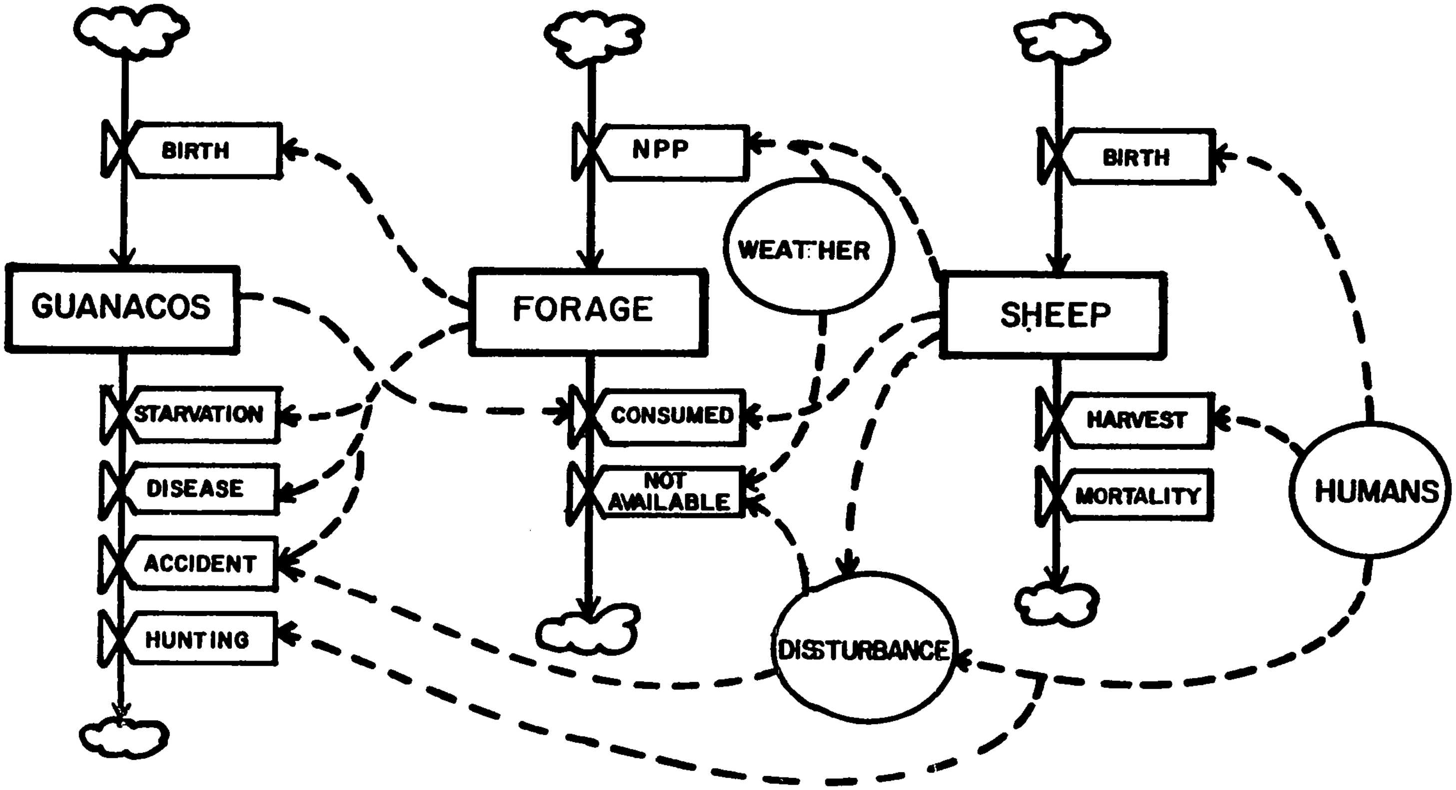

Figure 51. A model of the interastions of the guanaco, sheep, humans, and environment of the study area.

decomposition of the forage material either not available to the herbivores or not consumed.

In the model, three factors directly affect the guanaco population: forage supply, disturbance, and humans. The most important is clearly the forage supply which determines the rate of starvation, and influences the rate of birth, accidents, and disease. The human and disturbance factors are definitely secondary as they affect only the accident and hunting mortality rates (10% and and 5% of the total mortality).

The forage that is available to the guanaco population for growth and reproduction is affected by several factors. First, the NPP is affected by the abiotic conditions of the environment, such as soil fertility, climate, length of the growing season, and the herbivores themselves. Overgrazing by sheep has reduced the NPP of the Patagonian rangelands. Second, the forage supply is reduced by factors that make the forage unavailable to the herbivores, such as plant growth forms, weather patterns (i.e. snowfall that covers the forage), and social interactions with other herbivores (interference competition). The results of the present study have shown that social interactions between the guanaco and sheep and consumption by sheep have reduced the forage supply available to the guanacos by as much as 90 to 95%.

In the model, intraspecific competition is represented by the loop from the guanaco population to the rate of forage consumption, to the forage supply, then back to the rates of birth and death of the guanaco. This is the lop that ooperates to maintain the guanaco population within the limits established by interspecific competition.

Interspecific competition affects the guanaco in several ways. First, sheep have reduced the NPP of the range. Second, the sheep consume much of the preferred forage available to the guanaco and sheep. Third, social interactions with sheep (disturabance in the model) make much of the forage unavailable to the guanacos, and increase the accident rate. The reduction in the available forage reduces the birth rates and increases the mortality due to starvation, disease, and accidents.

This model of the results of the present study clearly shows that population regulation is not a simple process that can be neatly defined as density-dependent or independent. Rather, populations are limited by a number of factors both obvious and subtle. Furthermore, the relationship between these different factors over time undoubtedly changes as the environment changes, and must be periodically reevaluated during any process of population management.

In the case of the guanacos of Magallanes, if management of the guanaco is to be successful, steps must be taken to reduce the competitive pressures of sheep, and increase the forage supplies available to the guanaco.

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APPENDIX A

The Criteria of Age

The ability to accurately assign ages to individual animals in a population is a powerful tool in the study of that population. This ability permits the assessment of such important parameters as population structure, mortality and survival rates, age-specific reproductive rates, etc. While the major species of wildlife in North America, Europe, and Africa have been studied with regards to the criteria of age, no work has yet been completed on the guanaco, or any of the other South American members of the family Camelidae. For the present study, therefore, a method of age determination needed to be developed.

The objectives of the study of aging techniques were three: first, to determine the ages of the individual guanacos in the study samples by an accurate method; second, to develop an inexpensive field technique; and third, to develop accurate methods suitable for research.

All specimens used in this study were collected in the intensive study area of south-central Isla Grande. All skulls were critically examined for abnormalities that might make them inappropriate for this system. Skulls with abnormal wear or jaw disease were eliminated from the study group.

Three methods of age determination were analyzed in the present study: tooth replacement, tooth annulations, and tooth wear. These techniques will be discussed in the following sections.

Since the principal methods of age determination are based on dentition patterns, tooth wear, and tooth sectioning, a general description of the dentition of the guanaco is necessary. The guanaco, like most mammals, has heterodont dentition, that is the teeth are modified in shape and size to serve specialized functions in the tooth row. Four types of teeth are present: incisors (I), canines (C), premolars (PM), and molars (M). The guanaco dentition is also diphyodont, which means that they have both milk (or deciduous) teeth, and permanent teeth. The molars are the only teeth which are not preceded by milk teeth.

The general dental formula for the guanaco, following the standard terminology of Riney (1951) and Cockrum (1962) is the following:

$$\frac{\text{Incisors 003 \quad Canines 1 \quad Premolars 0234 \quad Molars 123}}{\text{Incisors 123 \quad Canines 1 \quad Premolars 0034 \quad Molars 123}}$$

The dentition of an adult male guanaco is shown in Figure 52. On the lower jaw, the mandible, we have three incisors, which are all of normal incisiform shape. They

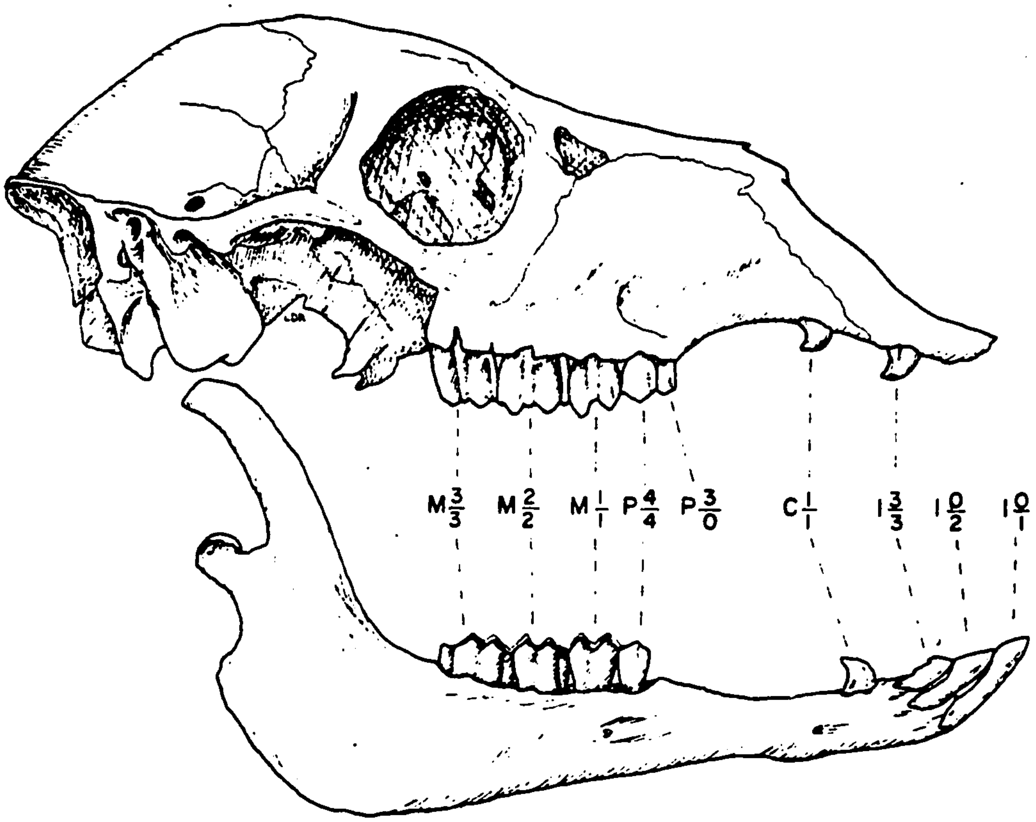


Figure 52. Dentition of an adult male guanaco.

are small, spatulate, and procumbent. The canines are of normal caniform shape. They are large and heavy in the male, and less so in the female. Premolars 1 and 2 are absent in all age classes. Premolar 3 is unicusped at birth, and is lost by the age one year, and is not replaced by a permanent tooth. Premolar 4 is tricusped at birth, and is replaced by a permanent unicusped tooth in adulthood. The three molars are selenodont molars, and are not preceded by milk teeth. The third molar has an additional tubercule, making it tricusped, while the first and second molars are bicusped.

On the upper jaw, the maxilla, the tooth numbers are reduced. Only the third incisor is present, and it has the form of a canine tooth. However, it arises from the premaxillary bone, and is therefore a modified incisor tooth. The canine is the same as on the lower jaw. The first premolar is never present. The second premolar is present as a unicusped milk tooth, but is not replaced by a permanent tooth. Premolar 3 is bicusped as a milk tooth, and is replaced by a permanent unicusped tooth, which is often lost in adulthood (after 3 years). Premolar 4 is bicusped both as a milk tooth and as a permanent tooth. The three molars are identical to the mandibular molars, except that the third molar is bicusped.

MATERIALS AND METHODS

Tooth Replacement

The pattern of tooth replacement was determined by examination of the dentition of known-age captive guanacos, "established-age" captive and free-ranging guanacos, and "established-age" guanaco mortalities.

The dentition of four known-age captive guanacos was monitored at regular intervals over a two year period. The animals were raised on natural forage. At the time of the initiation of the study, these guanacos were five, six, 18, and 19 months old. A total of 14 age records were collected from these individuals. Six other known-age guanacos were examined once each, two at birth, three at six months, and one at nine months.

The data from the known-age animals was augmented by examination of guanacos of "established-age". Since guanacos are born in a restricted period of time (85% are born in a 30 day period, see Chapter 7), the age of an animal with a known date of death could be calculated. The only error in aging such an animal would result from variation in birth dates for individual guanacos.

Robinette *et al.* (1957:135) used this method to establish ages of mule deer fawns, and noted that this would be be a "...source of error of less magnitude probably than individual variations in tooth replacement". The age of 60 guanacos varying in age from newborn to 30 months were established on this basis. Of these "established-age" animals, 46 were natural mortalities, 12 were live captures of free-ranging animals, and two were captive individuals.

Material collected from these sources compromised 77 records from 67 individuals, ranging in age from newborn to 51 months. In addition to this collection of known and established-age specimens, 177 sets of dentition were examined from other guanaco mortalities. These specimens were used to check for variations in the pattern of tooth replacement, and to augment the specimens for the descriptions of the various age classes.

Tooth Annulations

The teeth from 20 known-age guanacos were available for study: two individuals were pen raised, ages 3.5 and 9.5; and 18 individuals 2.5 years old were aged by tooth replacement. Skulls were obtained from an additional 172 guanacos, 3.5 years of age and older, that had died of natural causes. From each skull the first incisor and/or one canine was removed for sectioning. If necessary, the skull was soaked in warm water to facilitate tooth removal. The canines and incisors were chosen for study since these teeth were most readily removed, especially from live animals. Furthermore, initial study showed that the annulations from the roots from the molars were more difficult to interpret since the cementum layers were extremely compacted.

For the analysis of the annuli, the teeth were demineralized, sectioned, stained, and mounted on a permanent slide by a commerical laboratory, Matson's Commercial Microtechnique, Miltown, Montana. The methods used followed those of Lockard (1972) and Erickson and Seigier (1969). In general, the procedure was the following:

1. The root of the tooth was separated from the crown with a hacksaw.
2. The root was placed in a 30% formic acid solution for 72-96 hours to demineralize the tooth matrix.
3. This was followed by a neutralizing solution of lithium carbonate in 70% ethyl alcohol for 12 hours.
4. The root was sectioned on a longitudinal plane with a microtome, producing sections 12 microns thick.

5. The sections were stained with hematoxylin stain.
6. Permanent slides were made with Paramount or other mounting medium.

The mounted sections were examined with a compound microscope at 40 and 100 power, using transmitted light. All areas of the cementul were examined, since at some locations the cementum appeared to be damaged or removed.

Tooth Wear

During the course of the study of the guanaco's life history, 543 carcasses resulting from natural mortality were collected in the field, and an additional 25 live guanacos were collected for various studies. In each case, the complete skull, including the mandible was numbered and preserved. Of the total, 366 were adults over 2.5 years of age. An initial sample of 80 sets of dentition, representing varying degrees of tooth wear were aged by tooth annuli. These 80 sets of dentition were then grouped by year classes, and a detailed description was made of each year class in the sample, based on the degree of wear, using the system of Severinghaus (1949). A representative skull from each year class was then selected for use in comparisons with unknown age material.

After the year classes had been described, and a "known-age" collection established, each skull in the entire collection was then assigned an age on the basis of wear in comparison with the "known-age" representatives. After this was completed, a second sample of 117 guanacos was aged by a commercial laboratory on the basis of tooth annulations.

RESULTS AND DISCUSSION

Tooth Replacement

The orderly process of tooth replacement has been recognized as a means for aging animals since Xenophona, in 400 BC, described the process for the horse (Bigalke 1968). Recent studies have applied this process to a number of ungulate species, especially the cervids (Taber 1971, severinghaus 1949). The method is based on the observation that the deciduous, or milk teeth, are replaced by permanent teeth over a period of time, and that this process is highly correlated with age.

This technique has several advantages. First, it is very accurate, and the age of an animal can often be determined to the nearest month. Second, it is a simple technique requiring no special equipment or laboratory space, and trained technicians can readily age animals. A disadvantage is that most animals complete their replacement of deciduous teeth when they reach adulthood, often 2 or 3 years of age in ungulates, and no further ages can be determined.

The pattern of replacement of the deciduous teeth in guanacos appears to be very predictable, and highly diagnostic of age. In Table 35 the dentition of the known-age animals is summarized, and Table 36 contains the summary for the "established-age" animals. In both these tables, the data is limited to the mandible, since this is generally the most convenient for work in the field, and with the incisors present only on the mandible, this jaw is the more diagnostic for age. Table 37 summarizes the general tooth replacement pattern for both the mandible and the maxilla. In the following section, the dentition of the mandible of the different age classes is described, with special attention given to the key characteristics that differentiate the different ages. These descriptions should be cross referenced with Figure 53 which shows a typical mandible for each of the age classes.

Table 35. Tooth replacement patterns of the lower jaw for guanacos with age known.

				Incisors			Canine	Premolars		Molars		
Mos.	Wks.	No.	Sex	1	2	3	1	3	4	1	2	3
0	0	I171	M	-	-	-	-	-	-	-	-	-
0	0	I168	M	-	-	-	-	-	-	-	-	-
5	1	Gron	F	d	d	d	(d)	d	d	P	-	-
6	0	Pain	M	d	d	d	d	d	d	P	-	-
6	2	Gron	F	d	d	d	d	d	d	P	-	-
6	1	RG1	M	d	d	d	d	d	d	P	-	-
6	2	RG2	F	d	d	d	d	d	d	P	-	-
7	3	Gron	F	d	d	d	d	d	d	P	-	-
9	0	Gron	F	d	d	d	d	d	d	P	(P)	-
9	1	P1	F	d	d	d	d	d	d	P	(P)	-
17	1	Vivol	M	(P)	d(P)	d	d	d	d	P	P	-
17	2	I172	F	d(P)	d	d	d	d	d	P	P	-
18	0	I172	F	P	(P)	d	d	d	d	p	p	-
24	0	I172	F	P	P	P	(P)	d	P	P	P	P
24	0	Vivol	M	P	P	P	P	d	P	P	P	P
30	0	Vivol	M	P	P	P	P	-	P	P	P	P
30	0	I172	F	P	P	P	P	-	P	P	P	P
32	0	Vivol	M	P	P	P	P	-	P	P	P	P
39	0	I172	F	P	P	P	P	-	P	P	P	P
51	0	Vivol	M	P	P	P	P	-	P	P	P	P

Table 36. Tooth replacement patterns of the lower jaw in guanacos of "established" age.

Age				Incisors			Canine	Premolars		Molars		
Mos.	Wks.	No.	Sex	1	2	3	1	3	4	1	2	3
0	0	494	F	-	-	-	-	-	-	-	-	-
0	1	166	M	d	d	-	-	-	-	-	-	-
0	3	88	?	d	d	-	-	d	d	-	-	-
0	3½	87	?	d	d	(d)	(d)	d	d	-	-	-
0	4	223	?	d	d	d	-	d	d	-	-	-
1	2	207	?	d	d	d	(d)	d	d	-	-	-
2	0	154	F	d	d	d	-	d	d	(P)	-	-
4	2	309	?	d	d	d	d	d	d	(P)	-	-
5	0	5	?	d	d	d	-	d	d	(P)	-	-
6	2	192	?	d	d	d	d	d	d	(P)	-	-
6	2	190	?	d	d	d	d	d	d	P	-	-
6	2	191	?	d	d	d	d	d	d	P	-	-
6	2	194	F	d	d	d	d	d	d	P	-	-
6	2	293	?	d	d	d	d	d	d	P	-	-
7	0	140	?	d	d	d	d	d	d	P	-	-
7	0	193	?	d	d	d	d	d	d	P	-	-
7	0	86	F	d	d	d	d	d	d	P	(P)	-
7	0	114	F	d	d	d	d	d	d	P	-	-
8	2	G3	F	d	d	d	d	d	d	P	-	-
10	0	107	M	d	d	d	d	d	d	P	(P)	-
10	0	327	M	d	d	d	d	d	d	P	(P)	-
12	0	G6	M	d	d	d	d	d	d	P	(P)	-
12	0	G23	M	d	d	d	d	d	d	P	(P)	-
14	0	94	F	d	d	d	d	d	d	P	P	-
15	0	77	F	d	d	d	d	d	d	P	P	-
16	0	126	F	d(P)	d	d	d	d	d	P	P	-
17	0	117	F	dP	(P)	d	-	d	d	P	P	-
17	0	416	M	d(P)	d	d	d	d	d	P	P	-
17	0	G17	F	P	P	P	d	d	d	P	P	-
18	0	257	F	d(P)	P	P	d	d	d	P	P	-
19	0	174	M	dP	P	dP	d	d	d	P	P	-
20	0	262	F	dP	d(P)	d	d	d	d	P	P	-
20	0	282	F	P	dP	d(P)	d	d	d	P	P	-
20	0	46	F	P	dP	d(P)	d(P)	d	d	P	P	-
22	0	122	F	P	P	P	P	d	d(P)	P	P	(P)
22	0	318	M	P	P	P	(P)	d	P	P	P	P
24	0	164	M	P	P	P	P	-	P	P	P	P
24	0	287	M	P	P	P	P	-	P	P	P	P
26	0	141	F	P	P	P	P	-	P	P	P	P
27	0	G8	M	P	P	P	P	-	P	P	P	P
28	0	G12	M	P	P	P	P	P	P	P	P	P
30	0	220	F	P	P	P	P	#	P	P	P	P
30	0	269	F	P	P	P	P	#	P	P	P	P
30	0	279	F	P	P	P	P	-	P	P	P	P
30	0	218	M	P	P	P	P	d	P	P	P	P

Table 37. A summary of the patterns of tooth replacement in both jaws of guanacos.

MAXILLA

	INCISORS			CANINE	PREMOLARS			MOLARS		
AGE	1	2	3	1	2	3	4	1	2	3
Birth	-	-	0	0	0	0	0	0	0	0
1 mo.	-	-	0	0	D	D	D	0	0	0
3 mo.	-	-	D	D	D	D	D	(P)	0	0
6 mo.	-	-	D	D	D	D	D	P	0	0
9 mo.	-	-	D	D	x	D	D	P	0	0
10 mo.	-	-	D	D	x	D	D	P	(P)	0
15 mo.	-	-	(P)	(P)	x	D	D	P	P	0
18 mo.	-	-	P	P	x	D	D	P	P	0
24 mo.	-	-	P	P	x	P	(P)	P	P	(P)

MANDIBULA

	INCISORS			CANINE	PREMOLARS			MOLARS		
AGE	1	2	3	1	2	3	4	1	2	3
Birth	0	0	0	0	-	0	0	0	0	0
1 mo.	D	D	0	0	-	D	D	0	0	0
3 mo.	D	D	D	D	-	D	D	(P)	0	0
6 mo.	D	D	D	D	-	D	D	P	0	0
9 mo.	D	D	D	D	-	D	D	P	0	0
10 mo.	D	D	D	D	-	D	D	P	(P)	0
15 mo.	(P)	D	D	(P)	-	D	D	P	P	0
18 mo.	P	P	(P)	P	-	D	D	P	P	0
24 mo.	P	P	P	P	-	D	P	P	P	P
Adult	P	P	P	P	-	x	P	P	P	P

Key: 0 tooth not yet errupted
D deciduous tooth
P permanent tooh
( ) tooth errupting
x tooth lost, and not replaced by permanent

Figure 53. Tooth replacement in guanacos. The ages marked on the jaws are the age in months.

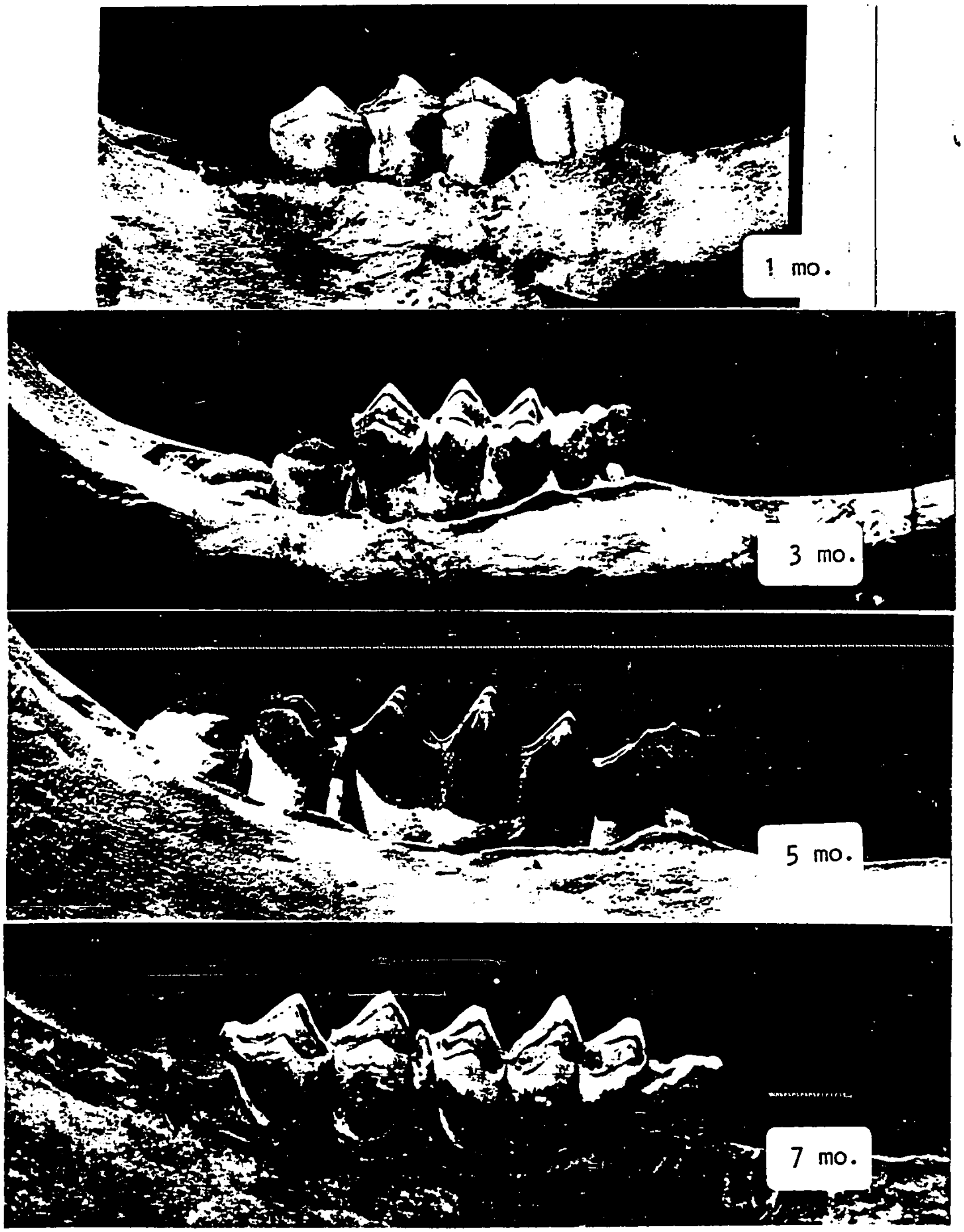


Figure 53. Continued.

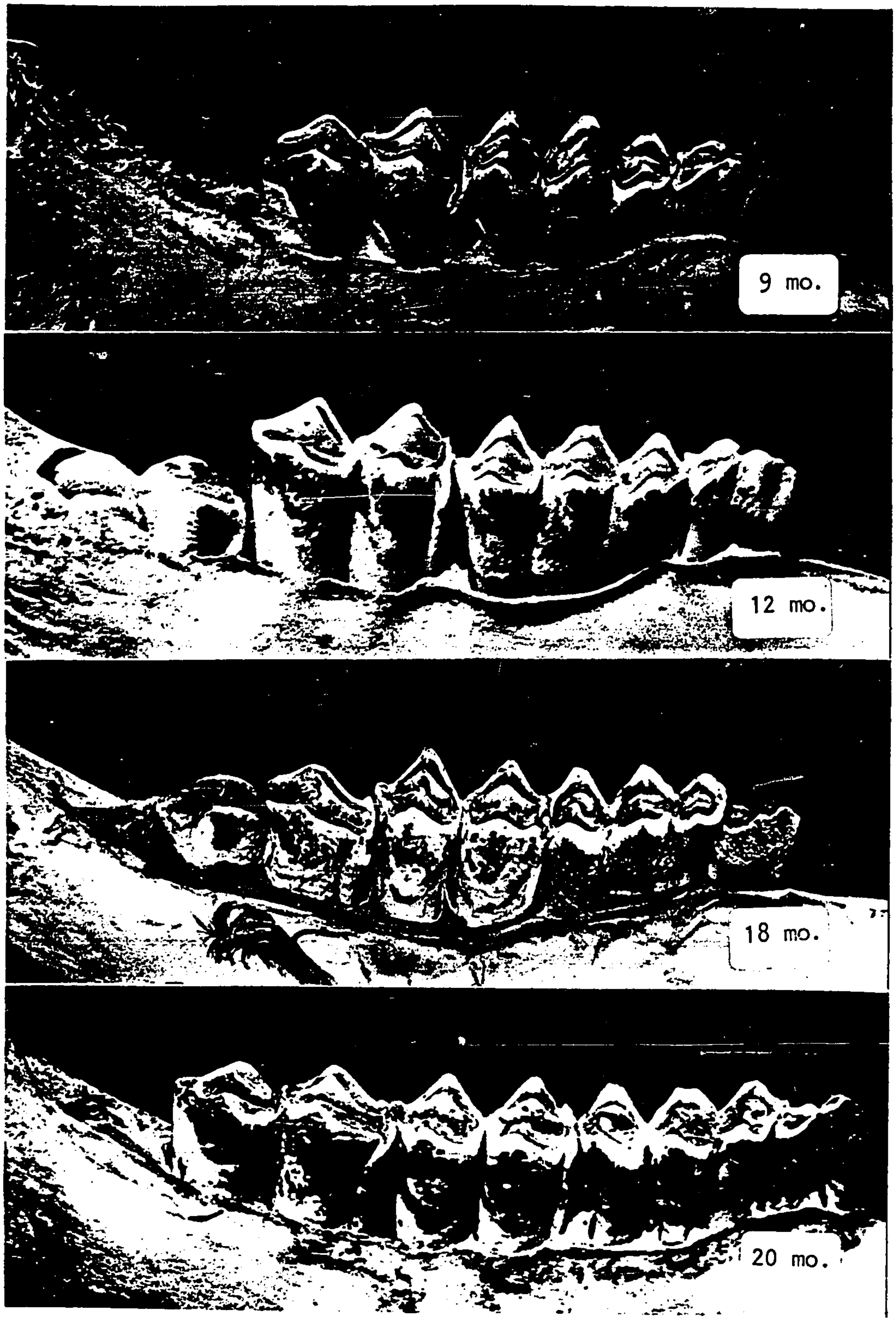


Figure 53. Continued.

Tooth Replacement Age Class Descriptions

BIRTH. No teeth had erupted through the gum although all three deciduous incisors and the two deciduous premolars were through the jawbone.

ONE WEEK. The first two incisors were through the gum; I1 was 2.3 mm and I2 was 1.3 mm in height, measured on the buccal side. I3 was just about to cut through the gum. The premolars, canine, and molars had not yet erupted, however, the premolars were through the jawbone. The lower jaw length, measured from the mental-foramen to the posterior corner of the jaw articulation (see Figure 14) averaged 113.0 mm.

ONE MONTH. The incisors showed considerably more growth, measuring I1 6.1 mm, and I2 3.2 mm on the buccal side. I3 was still in the process of erupting through the gum. The premolars had now broken through the gum, and the gumline was at the shoulder of PM3. The heights were PM3 6.6 mm, and PM4 9.0 mm on the lingual side. No canines or molars were erupted. On defleshed skulls the alveolus could be seen for the first molar. The average jaw length was 121 mm.

TWO MONTHS. All deciduous incisors had erupted with the following measurements on the lingual side: I1 10.1 mm, I2 7.8 mm, and I3 2.5 mm. No wear was visible on the incisors. The deciduous canine was present in several cases, but the eruption of this canine was erratic, and not well correlated with age. The premolars showed slight wear, with the maximum cusp width (occlusal surface) of 1.5 mm on PM4. The average lower jaw length was 133 mm.

THREE MONTHS. The deciduous incisors were three-fourths developed, and still showed no wear. Slight wear was seen on PM4, and the premolars were only one-half developed. The key characteristic of this age class was the eruption of the first molar. One cusp was through the gum on four of seven specimens, with a maximum buccal height of 4.0 mm on the anterior cusp. The average lower jaw length was 141.0 mm.

FIVE MONTHS. The incisors showed slight wear for the first time. The premolars reached maximum height, and had now started to be worn down. PM4 showed medium wear with a width of 3.0 mm on the occlusal surface. The first molar was through the gum on all of the skulls examined with one cusp, and both anterior cusps on six of eight skulls. The maximum height was 8.5 mm on the lingual anterior cusp, and the minimum for the same cusp was 6.5 mm. The average jaw length was 149.0 mm.

SIX MONTHS. The first molar was now even in height with the PM4, and showed slight wear; 2.5 cusp width on the anterior lingual cusp. The alveolus of the M2 could be seen in the jaw of defleshed skulls. The average lower jaw length was 152.0 mm.

SEVEN TO EIGHT MONTHS. The third premolar showed wear for the first time at seven month. PM4 was worn heavily, and the infundibulum was worn to a thin line with the lingual and buccal cusps separated by less than 1 mm. The first molar was fully developed, with a height of 12 mm on the lingual side, and was slightly worn with an occlusal surface width of 2-3 mm. The second molar could be seen in the jawbone, and the anterior lingual cusp was above the jawbone on one of five skulls examined. The average lower jaw length was 168.0 mm.

NINE TO FIFTEEN MONTHS. On defleshed skulls the alveolus of the permanent incisors could be seen at nine months. The permanent incisors could be seen in the jaw of many specimens, but this was erratic. The wear on the deciduous premolars was heavy, and the infundibulum was no longer longitudinally continuous on PM4. The key characteristic of this age class was the eruption of the second molar at 10-11 months, when all specimens had at least one cusp through the gum. At 14 months the anterior lingual cusp had a height of 8.0 mm. The lower jaw length averaged 175 mm at 10 months, and 183 mm at 15 months.

SIXTEEN TO TWENTY MONTHS. In this age class, the deciduous incisors were all replaced by the permanent teeth. The replacement was rapid, and necessarily so since the guanaco must obtain most of its food with these teeth. The replacement order was I1 first, I2 second, and I3 last. At 16 months the first permanent incisors had begun to cut through the gum. The other incisors could be seen in the jaw on defleshed skulls. At 20 months the I1 measured 20.0 mm on the buccal side, and I2 measured 8.5 mm. I3 was only slightly erupted at this time. On many skulls both deciduous and permanent incisors were present at the same time, and the deciduous teeth were lost somewhat earratically. The permanent canines began to errupt at 16 months, and most specimens had permanent canines at 24 months.

At 16 months the jawbone at the base of both deciduous premolars could be seen to be erroding away form the tooth. At 20 months the permanent PM4 could be seen beneath the deciduous tooth in the jaw. Also at 16 months, the first molar was fully developed, and the second molar was three-fourths developed, with the gumline at the shoulder of the tooth. The third molar could be seen in the alveolus on defleshed skulls. The average jaw length was 190.0 at 20 months.

TWENTY TO TWENTY-SIX MONTHS. The permanent incisors were all complete, and fully developed by 24 months. Measurements at 24 months on the buccal side were I1 20.0 mm, I2 18.0 mm, and I3 12.0 mm. On most specimens the permanent canines were at least in the process of erupting, with many already completed. Female canine teeth were generally less advanced in development.

At 22 to 26 months the PM4 was lost and replaced by a permanent tooth. The exact age of replacement was irregular. PM3 was also lost at this time, but in many animals it was retained until four or five years of age. It was not replaced by a permanent tooth.

At 22 months the third molar was at the level of the gumline. It erupted rapidly, and at 24 months was half developed and the anterior lingual cusp measured 10.1 mm in height. At 26 months the M3 was three-fourths developed, and showed slight wear on the anterior lingual cusp.

The averge lower jaw length was 196.0 mm for this entire age class.

THIRTY MONTHS. The primary characteristic of this age class was the condition of the PM4 and M3. The permanent PM4 was not yet fully developed, was below the level of the first molar, and showed no wear.

The third molar was not yet fully developed, and the alveolus had not yet closed aroung the base of the tooth. Wear on the second cusp was slight, and only on the anterior cusp. Since the elongation of the mandible was not completed, the gumline around the posterior cusp had not retracted enough to expose the full height of the tooth, and in some cases the third cusp was not erupted through the gum. The position of the third molar gave the impression of being cradled in the angle formed by the jaw and the ramus of the jaw.

There was only slight wear on the M1 and M2. The sides of the infundibulum formed a broad and conspicuous "V". On all teeth the enamel layer was thicker that the visible dentine layer.

Discussion

The technique of age determination by means of tooth replacement is based on the assumptiuon that the tooth replacement is a regular and predictable process that is correlated with the age on the individual. The results of the present study show that except for minor variations, the process is quite regular. Thus, the age classes that have not reached full adult dentition, those between birth and three years of age, can be aged by tooth replacement patterns with confidence.

However, in other studies, the rate of tooth replacement was found to be influenced by the nutritional levels of the population. Geist (1971) reported that different bighorn sheep populations had different rates of tooth replacement. He postulated that those on better ranges, under less crowded conditions, were better nourished, resulting in larger body size and more rapid physical developement, including the replacement of the deciduous teeth. Severinghaus (1949) and Robinette *et al.* (1957) also found nutrition to be a factor in tooth replacement in cervids. They noted that errors could result if a system developed for one population or geographic region is applied to a different region without local varification of the method. Thus the descriptions given above for the guanaco of Isla Grande may not be appropriate for northern Chile.

Tooth Annulations

The technique of age determinaton through the analysis of annulations in the cementum of the teeth of artiodactyla has gained prominance with wildlife investigators. The initial studies of Schaffer (1950) and Laws (1952) on marine mammal tooth annulations were followed by studies on major wildlife species such as deer, wapiti, moose, goats, bears, sheep, caribou, lynx, pronghorns, and even man (Low and Cowan 1963, Reimers and Nordby 1968, Sargeant 1967, McCutchen 1969, and Taber 1971). Recent studies have improved on the technique and have greatly simplified the methodology and increased the precision (Erickson and Seliger 1969).

The results of the present study are consistent with earlier successful studies of tooth annulation. The number of annuli in the tooth sections from the known-age animals strongly indicate that one set of light and dark annuli are added each year throughout the animals lifetime. Growth layers in the dental cementum appear as alternate light (opaque) and dark (translucent) layers. A complete annual increment consists of one light and one dark layer. "These layers result from the periodic seasonal differences in the rate of deposition of cementoblasts. The opaque zone - representing concentrations of cementoblast cell bodies..." (Wolfe 1969:429). In the guanaco the white zone is laid down in the spring and summer and the dark zones are deposited in the fall and winter.

The annulations in the root of the first incisor of a female guanaco, 3.3 years old is shown in Figure 54. This female was collected in the fall, and at this time the dark layer has begun to form, and the white layer has terminated growth. The first dark layer, marked "A" in the figure is the dentino-cementum junction. This layer is very distinct in both incisor and canine teeth sections (see Figure 55).

This sequence of light and dark layers continues throughout the life span of the guanaco, however, in the later years, the layers in the cementum are more compacted, and less distinct. Figure 55 gives the cross section from a canine of a 9.5 year-old male guanaco. In this individual, the layers are progressively thinner.

Figure 54. Cross section of the root of an incisor from a female guanaco 3.3 years old.

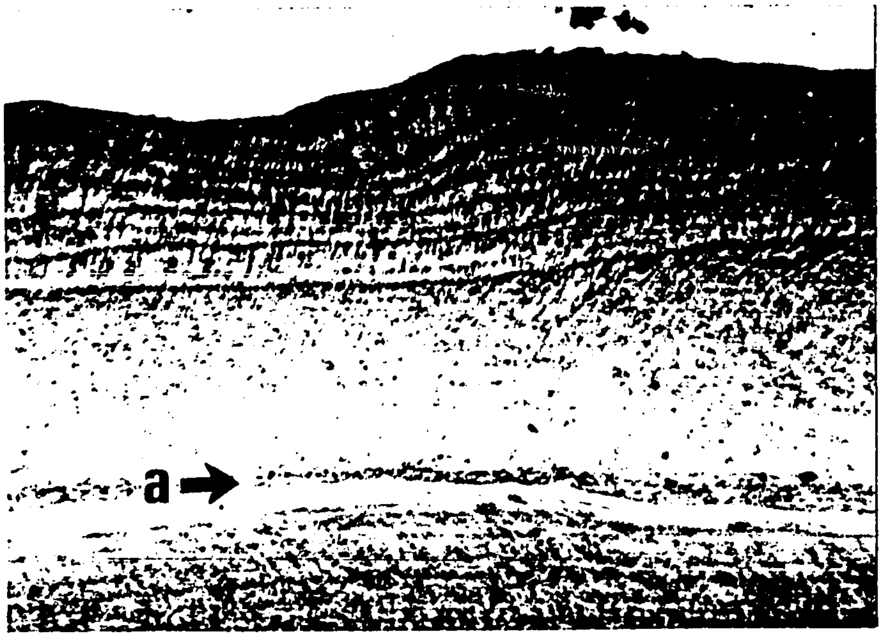


Figure 55. Cross section of the root of a canine from a male guanaco 9.5 years old.

however, they remained distinct throughout the life of the animal.

Since the first permanent incisor and the permanent canine teeth erupt at the age of 18 and 15 months respectively, the first white layer after the dentino-cementum junction is formed during the summer of the second year of life. Therefore, the age of the guanaco can be determined by using the first dark layer as age 2.5 years, and the age is the total number of dark layers plus one.

The cementum annulations on the canine teeth of the males were consistently easier to interpret than those from the incisors. In most cases the cementum layers showed a great degree of separation. However, in the females, the incisor was more readily interpreted, since the canine teeth are greatly reduced in size. In all teeth, the best area for counting the annuli was the portion of the tooth termed the "boss" by Low and Cowan (1963), or where fluting is present.

Within each light zone, several darker lamellae can be distinguished (see Figure 55). These are similar to those described by Low and Cowen (1963:469), who hypothesized that they "..may result from fluctuations in food intake or from deep-seated rhythmic growth". However, the significance of these lamellae is still unknown. The difference between these secondary layers, and the normal annuli is readily apparent, and they should not complicate age determination.

The results of the present study, and the others cited, indicate that the annuli of teeth from animals in temperate environments are highly correlated with age, and can be used as an accurate means of age determination. This technique should be generally applicable to guanacos throughout their temperate range in southern Patagonia. However, the method needs to be reevaluated for the guanacos that are found in the northern arid and non-temperate regions, to establish the pattern of annuiations appropriate to the regional environmental circumstance (Low and Cowan 1963).

Tooth Wear

With the development of tooth annulation aging techniques, the determination of age on the basis of tooth wear has been virtually discontinued. Objections to the system based on tooth wear are that: 1. It is often difficult to age the older age classes due to excessive wear; 2. Teeth are worn down at different rates from areas to area, depending on the amount of abrasive material in the diet; 3. The key characteristics used are often subjective; 4. The results are often inconsistent with results from annuli methods (Ransom 1966, Keiss 1969, Wolfe 1969, and others).

While these objections are no doubt valid, there are circumstances when the tooth annuli technique is neither practical nor appropriate. Furthermore, not all investigations of tooth annuli have been successful. Robinette _et al_. (1977) list six studies of cervid annuli aging that had success rates varying from only 50% to 75% when compared to known age animals.

In the following section, the mandibular dentition wear patterns are described and illustrated. The key characteristics that distinguish the age classes are noted. The descriptions are based on the average total amount of wear on the tooth row, and some individual variations are to be expected. An individual specimen should not be aged on a single characteristic, but rather on the overall wear.

Descriptions of the age classes over 11.5 years are not given, since the results show that these year classes can not be reliably separated on the basis of wear. Each of the age classes from 3 to 10 years of age is given, accompanied by a photograph of a representative specimen of that age class. Figure 56 shows this photographic series. Most descriptions are based on winter mortalities, that is animals that are 3.5, 4.5, 5.5, years old, etc.

Wear Class Descriptions

THREE AND A HALF YEARS. The primary condition that distinguished this age class was the condition of the third molar and the fourth premolar. The fourth premolar had now completed development, but showed only slight wear. The enamel was not worn through on most specimens.

The posterior cusp of the third molar still showed no wear. The middle cusp had a narrow line of dentine visible where the enamel had been worn through, on the lingual crest. However, this dentine line was still narrower than the enamel layer.

Figure 56. Tooth wear by age in guanacos. The ages shown are in years.

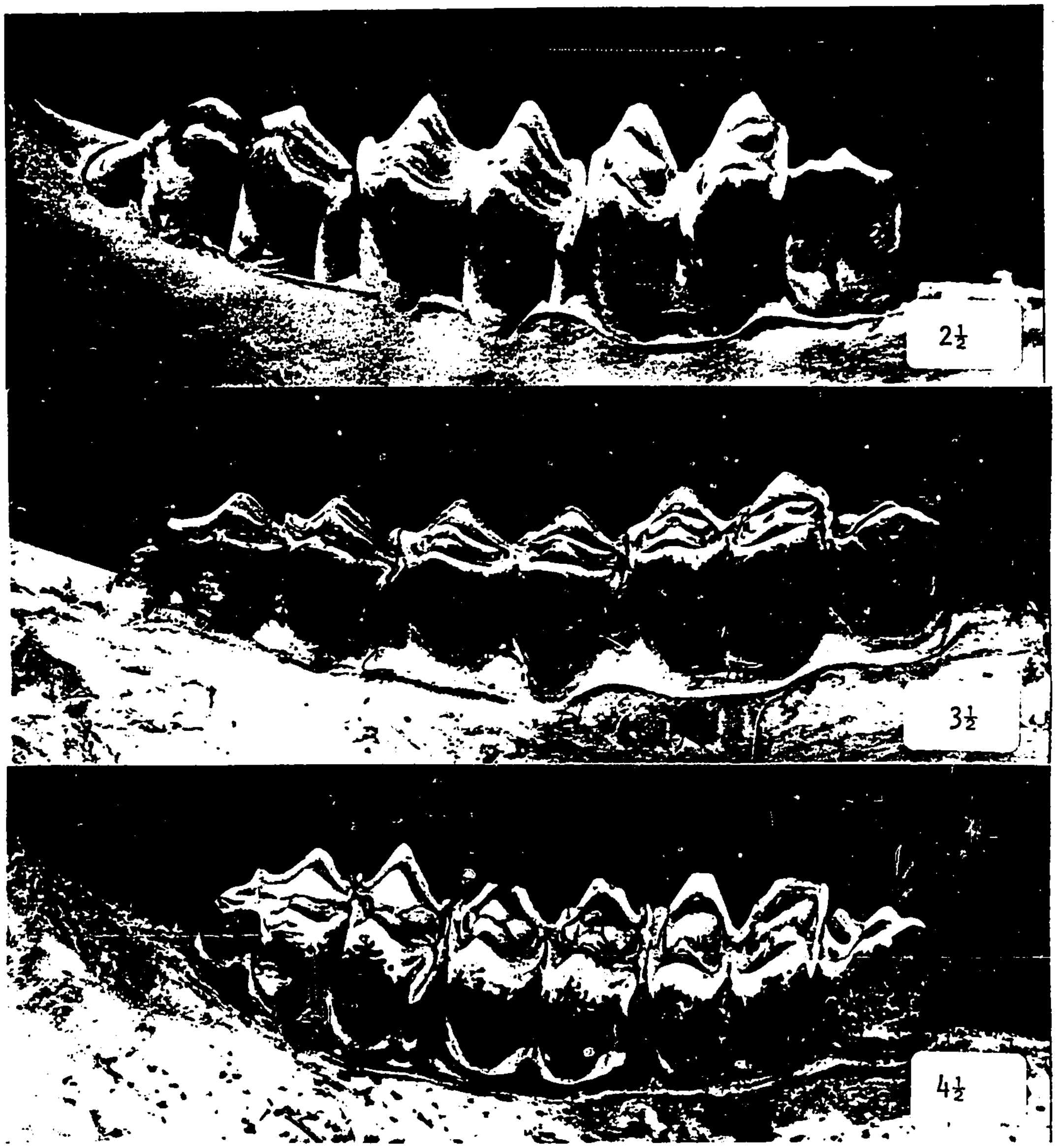


Figure 56. Continued

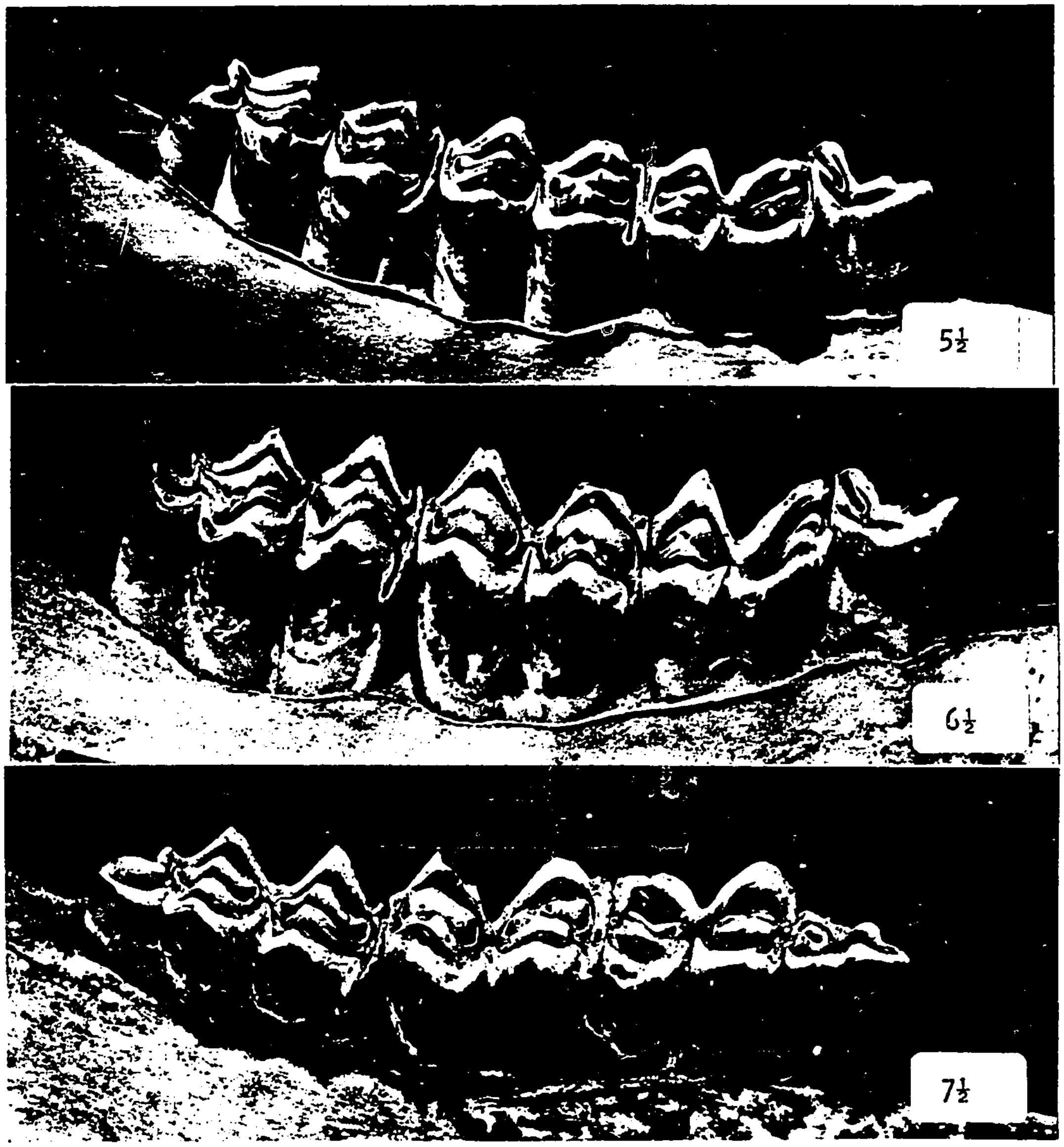
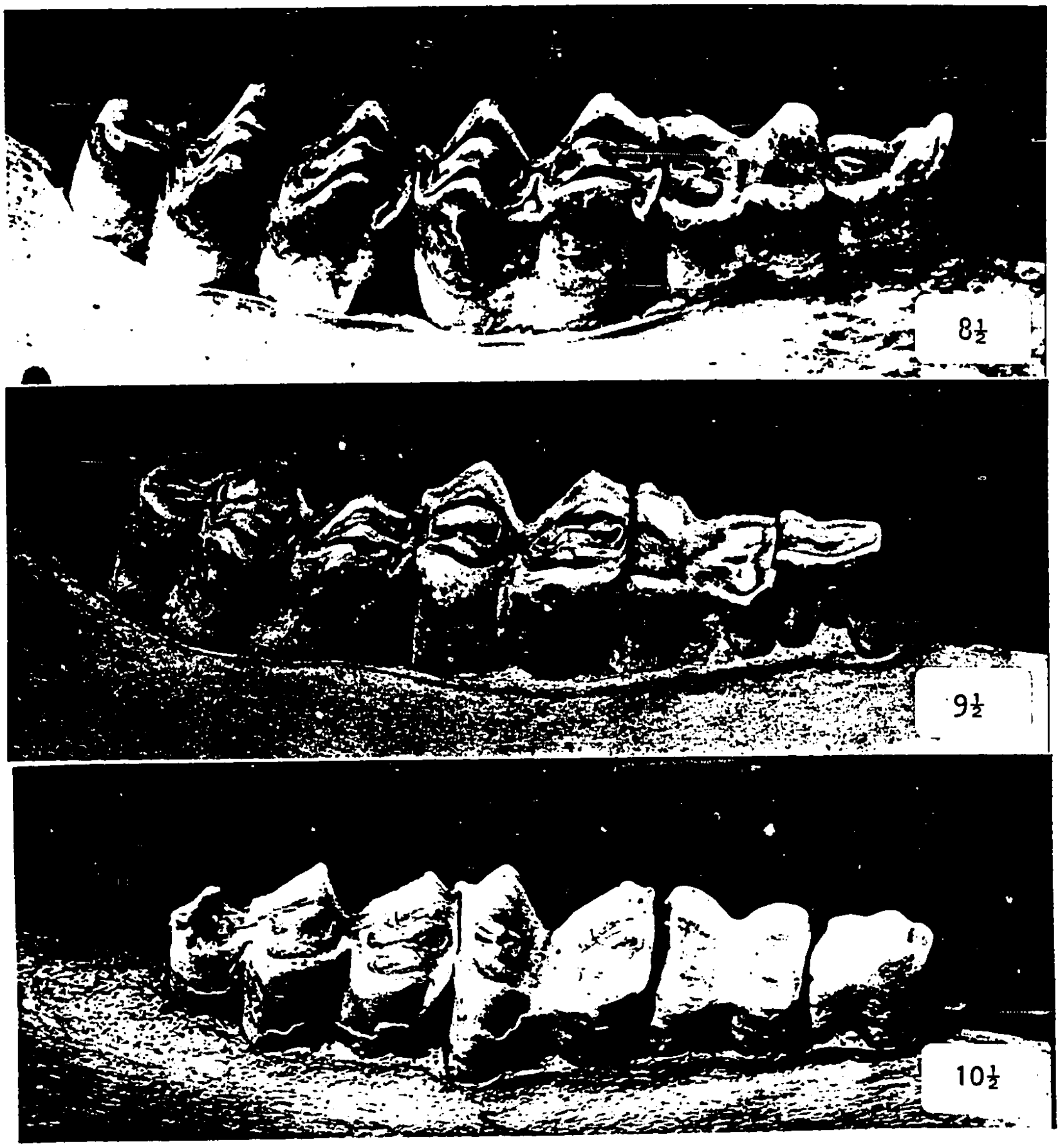


Figure 56. Continued.



On the anterior lingual cusp of the M2 the dentine width was equal to that of the enamel, but overall wear was less than that on the posterior cusps. On both cusps of M1 the dentine was slightly wider than the enamel. On both M1 and M2 the lingual crests were still high and pointed, and the infundibulum was still a broad deep "V".

FOUR AND A HALF YEARS. The primary character for this class was the condition of the PM4, and the posterior cusp of M3. The wear on PM4 was now moderate, with the occlusal surface measuring 3 to 5 mm in width.

The M3 was now completely developed, with slight wear on the posterior cusp. The occlusal surface of this cusp measured an average of 1.5 mm in width. On the second cusp on the lingual side, the dentine width was still less than that of the enamel, but on the buccal side the two were equal in width.

Only a thin, shallow crescent groove remained of the infundibulum on M1. The wear was moderate on both M1 and M2, with the cusps still very crested. The enamel was still complete in the area of the constriction between the cusps on all molars.

FIVE AND A HALF YEARS. This age class was distinguished by the condition of the first molar. The wear was moderate, with the infundibulum reduced to a groove, approximately one-half its former length. The dentine on the anterior lingual cusp was two to three times the width of the enamel. The enamel was discontinuous in the constriction between the cusps, with dentine showing where the enamel had been worn away.

On the second molar the dentine was wider than the enamel on all cusps, and the infundibulum was greatly reduced. The infundibulum of the M3 was no longer continuous from the anterior to the posterior cusp. It was now a crescent shaped groove on both cusps. The width of the dentine was equal to that of the enamel on the posterior cusps.

The infundibulum of the PM4 was worn to an oval groove, and the general wear was moderate.

SIX AND A HALF YEARS. The primary characteristics of this class were the condition of the M1 and the condition of the enamel separating the cusps on all molars. The first molar was now almost worn flat, with the infundibulum remaining as just a slight line on both cusps, less than half of its original length (now just three to five mm in length). The occlusal surface was deeply scooped in shape, and the lingual crest was worn away on the anterior cusp.

The dentine between the cusps of the first molar was equal to the width of the enamel. On the second molar, the enamel was discontinuous between the cusps, with the dentine just a narrow line. On the third molar the enamel was still continuous, and only moderate wear showed on M3.

SEVEN AND A HALF YEARS. The key characteristic of this age class was the wear on the first and second molars. The M1 was worn flat with no difference between the lingual and buccal crests, except for a slight slope from the lingual to buccal side. The infundibulum remained as just a line on the anterior cusp. This age class had the maximum possible wear with the infundibulum still remaining on the anterior cusp.

On the M3 the enamel betwen the cusps was now discontinuous. The dentine was wider than the enamel on the posterior cusps.

The infundibulum of the PM4 was worn away, and remained as a small circle about 1.5 mm in diameter, with no depth.

EIGHT AND A HALF YEARS. In this age class the key characteristic was the condition of the first molar. The M1 was now worn heavily, with the infundibulum completely worn from the anterior cusp, and reduced to one-third its former length on the posterior cusp.

The cusps of the M2 and M3 were still well defined. On M3 the dentine was two to three times the width of the enamel on the posterior cusp, and general wear was heavy.

NINE AND A HALF YEARS. The key characteristic of this age class was the condition of the first molar. Both cusps were now worn completely flat, with no infundibuli remaining, except for an occasional slight spot on the posterior cusp. The height of the tooth was 4.0 mm from the gumline on the buccal side.

The infundibulum was completely worn from the PM4.

On M2 and M3 the infundibuli were still complete, crescent grooves with slight depth, and discontinuous between the cusps. The posterior cusp of the M3 was scooped out, and had a width of six to eight mm.

TEN AND A HALF YEARS. The primary characteristic of this age class was the condition of the first and second molars. The M1 was worn to the gumline and the occlusal surface was narrower than at eight or nine years. On several specimens only dentine remained, as all enamel had been worn away.

The second molar had the infundibulum reduced to one-forth its original length, but was still present.

Comparison of Annuli and Wear Methods

The comparison of ages based on tooth cementum annulations and tooth wear patterns showed that the wear characteristics were moderately accurate over restricted age classes. For this comparison, the age of each specimen as determined by annuli was assumed to be correct, and any deviations were considered to be improper aging by wear criteria.

When all age classes are included, the tooth wear aging method correctly classified 35.5% of all guanacos; 69.1% were within one year of the annuli age; and 82.3% were within two years. However, only one individual of 20 in the ages over 11 years was correctly aged, and in general in mature individuals, the wear ages were a gross underestimation of annuli ages. Hence the conclusions of Ransom (1966) and others were correct for the older age classes; wear in the very old age classes is irregular or too excessive for proper aging by wear.

When the same comparison is restricted to the two to ten year old age classes, which comprised 86% of the total sample, the results improved: 46.2% were aged correctly; 79.8% were within one year of the annuli age; and 93.3% were within two years. Furthermore, while a large part of the sample was misaged, the errors tended to be compensating, since the comparison of the ages as determined by annuli and wear, by means of a paired "t-test" failed to show any significant difference between the means ($P=0.05$, with a sample size of 161). The mean ages based on the annuli method was 5.82, and for the wear estimates it was 6.02. There appears to be a slight but non-significant bias for over estimation of the age by the wear method in these younger individuals.

Unfortunately, the second sample of specimens aged by the annuli method were sectioned and interpreted after the wear estimates were made, and the skulls were no longer available for reexamination. It is possible that further study of the misaged skulls could have improved the accuracy of the system.

An attempt was made to improve on the wear aging system through the use of the molar wear ratios system of Robinette _et al_. (1957). However, the overlap in age class ratios was as much as five to six years, thus making the technique useless for this species. The main reason for the overlap could have been due to the lack of a distinct and regular gumline from which to measure the height of the tooth.

The accuracy of the guanaco tooth wear method is comparable to that of other studies using both tooth wear and annuli. Keiss (1969) found that trained biologists correctly aged 51.9% of elk on the basis of wear with the use of a "jaw-board". Using annulations, hoth Low (1967) and Robinette _et al_. (1977) were able to correctly age red deer and mule deer respectively only about 50% of the time.

CONCLUSIONS

The estimation of the age of mammals by tooth annulations has largely supplanted the other methods due to the greater accuracy of the method. While the annuli method appears to be generally more reliable, it is limited in application since it is not a simple field method, and the costs are often prohibitive. Hence in certain circumstances, especially in developing countries, other techniques may be more appropriate.

Guanacos that have not attained a full complement of fully erupted permanent teeth can be aged with considerable accuracy on the basis of tooth replacement. Most animals can be aged to the nearest month of age. Determination of age in guanacos with full dentition is most accurately accomplished through an analysis of cementum annuli in the first incisor or canine tooth. Determination of age on the basis of tooth wear is subject to definite limitations. Guanacos over the age of ten years could not be accurately aged on the basis of wear in the present study, and must be aged by annuli. However, guanacos in the three to ten year-old group were aged correctly 46.2% of the time, and errors tended to be compensating. The resulting age distributions from annuli and wear based ages were not statistically significant (Chi-square goodness-of-fit test, with P=0.05). It is possible that with continued study and refinement of the wear class descriptions, that increased accuracy could be achieved from the wear method.

Before one attempts a detailed breakdown of the ages of ungulates beyond the age of three years, they should make reasonably sure that the increased effort is justified. In many instances, especially managerial situations, there is little reason to attempt to age ungulates by annuli, except in the older age classes, or animals of special interest, such as females collected for age-specific reproductive studies. Tooth erruption and wear, when properly undertaken, can often yield reasonably acceptable results.

Before the results from this study are used throughout the range of the guanaco, local studies need to be undertaken to validate their use in that location. This is especially true in the northern, less temperate parts of the guanaco range, where annuli in the cementum may not be related to an annual cycle of seasons. Wear patterns are particularly vulnerable to change from region to region due to changes in the amount of abrasive material in the diet. Tooth replacement is less variable, but is also a function of diet.

APPENDIX B.

Calculation of the Competition Coefficients

The general definition of a competition coefficient is a "number giving the degree to which an individual of one species affects through competition the growth or equilibrium level of a second species' population, relative to the effect of an individual of the second species" (Schoener 1974d:332). In this study the competition coefficients are based on the resource utilization functions for forage and habitat, given in Table 31 and Figure 44, respectively. A one-dimentional competition coefficient is calculated for each resource, and since the resources are interdependent they are combined into a "multidimentional" coefficient by a weighted linear combination of the form:

$$A_{ij} = \frac{1}{2} \left(A_{ij}(F) + A_{ij}(H) \right) \qquad (21)$$

where the A is the coefficient, and F and H are the forage and habitat resources.

The forage resource data were used to calculate the competition coefficient by the method of Schoener (1974d), given by the formula:

$$A_{ij} = (T_j/T_i) \frac{\sum (d_{ik}/f_k)(d_{jk}/f_k)(b_{ik})}{\sum (d_{ik}/f_k)^2(b_{ik})} \qquad (22)$$

> "where Tj/Ti is the ratio of the number of items consumed by an individual of species j to that consumed by an individual of species i measured over an interval of time that includes all the regular fluctuations in consumption for both species; f_k is the standing frequency of the resource k in the environment; b_{ik} is the net calories gained by an individual of species i for an item of resource k; and the summations are taken over all resources eaten by at least one of the competing species" (Schoener 1974d:339).

In this study, the assumption is made that the caloric values of the different forage items are identical for both species of consumers, and they cancel out of the equation. Since all parts of the grass plants are eaten including the stems, and only the new growth of the browse is consumed, the nutritional values for the different forage classes should not be greatly different (Stoddart *et al.* 1975). Also, there is little evidence to indicate that the sheep and guanacos should vary in their ability to digest a given forage type (Stoddart *et al.* 1975).

To use this formula for calculating the competition coefficients, one must assume tht either the consumers are at equilibrium levels, or that the resources are close to equilibrium for given values of the consumers. This latter assumption is generally true, especially for ungulates and their resources, since the resources respond quickly to changes relative to the consumer (Schoener, per. comm.).

The seasonal availabilities of the forage classes used in the calculations of the seasonal coefficients are given in Table 38. These were calculated on the basis of

Table 38. Relative seasonal availabilities of the different forage classes within the study area, Isla Grande, Chile.

Month	Grass	Grass-likes	Browse	Forbs
February	48.9	16.4	32.5	2.3
April	47.8	17.5	32.6	2.1
June	42.5	20.1	37.6	0.8
September	10.0	12.0	77.0	1.0
October	27.2	15.2	56.4	1.2
December	44.4	15.0	37.6	3.0

the estimated initial and final frequencies in the environment, and the seasonal consumption patterns from the food habits data.

The habitat competition coefficients were calculated by the method of MacArthur and Levins (1967), as follows:

$$A_{ij} = \frac{\sum P_{ih} P_{jh}}{\sum P_{ih}^2} \qquad (23)$$

where P_{ih} is the relative use of the habitat type h by species i. The summations are taken over the range of habitat types occupied by at least one of the competing species.

APPENDIX C.

Key to Symbols

The following are the symbols and meanings for Schoener's (1974c) model of competition:

C_i -Maintenance and replacement cost of an individual of Competitor i.

I_{Ei} -Rate of net energy input into population of Competitor i of resources exclusive to that comsumer.

I_{0i} -Rate of energy input into the system usable by both Competitors, in units of energy for Competitor i.

N -Number of individuals in the population.

r_i -Number of individuals resulting from the conversion of one unit of net energy input for Competitor i.

B -Likelihood of an individual of Competitor 2 getting an item relative to an individual of Competitor 1.

VITA

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Personal

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Parentage:	Gerhard and Eloise Raedeke

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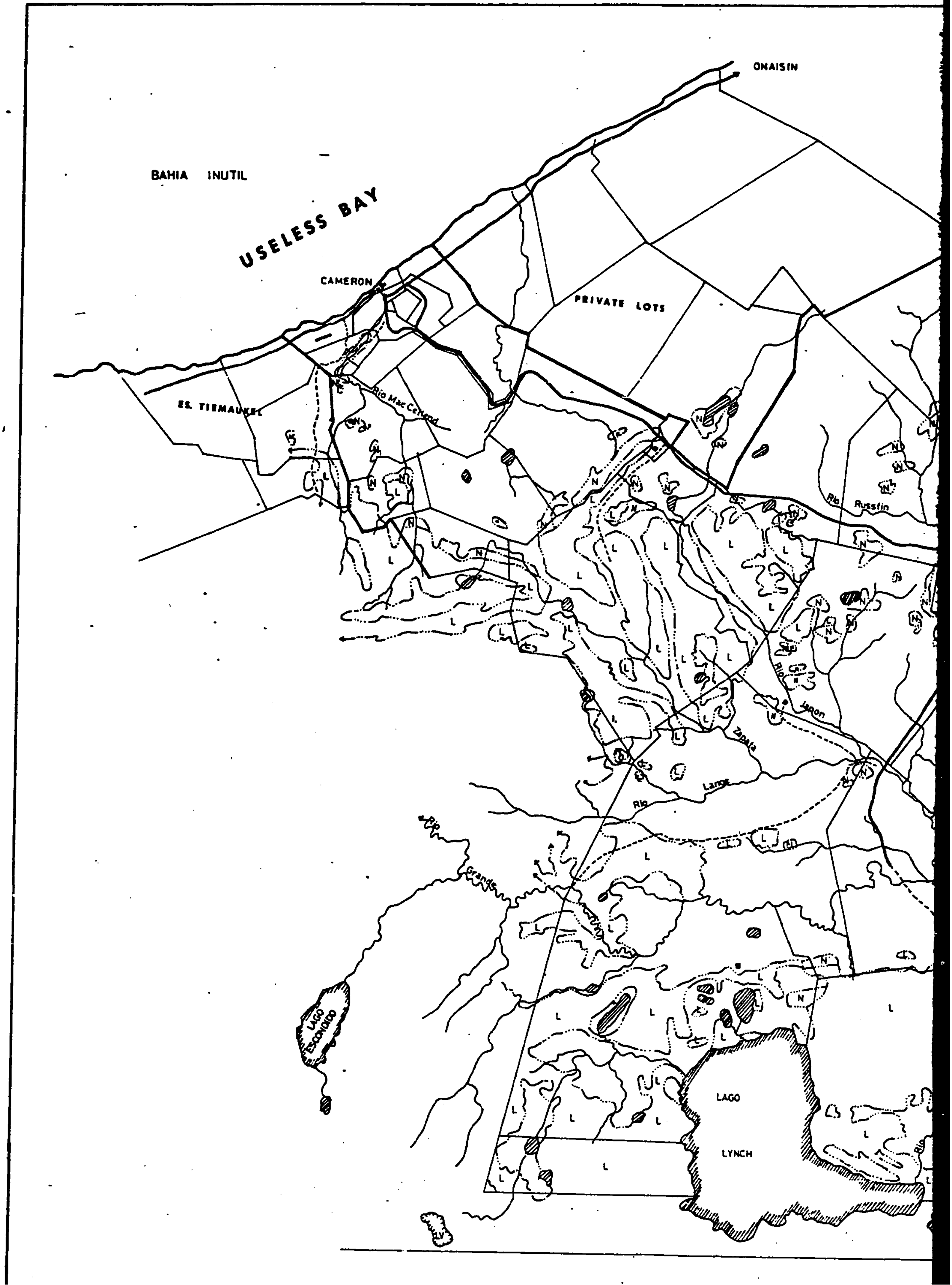
Bachlor of Science:	University of Montana Missoula, Montana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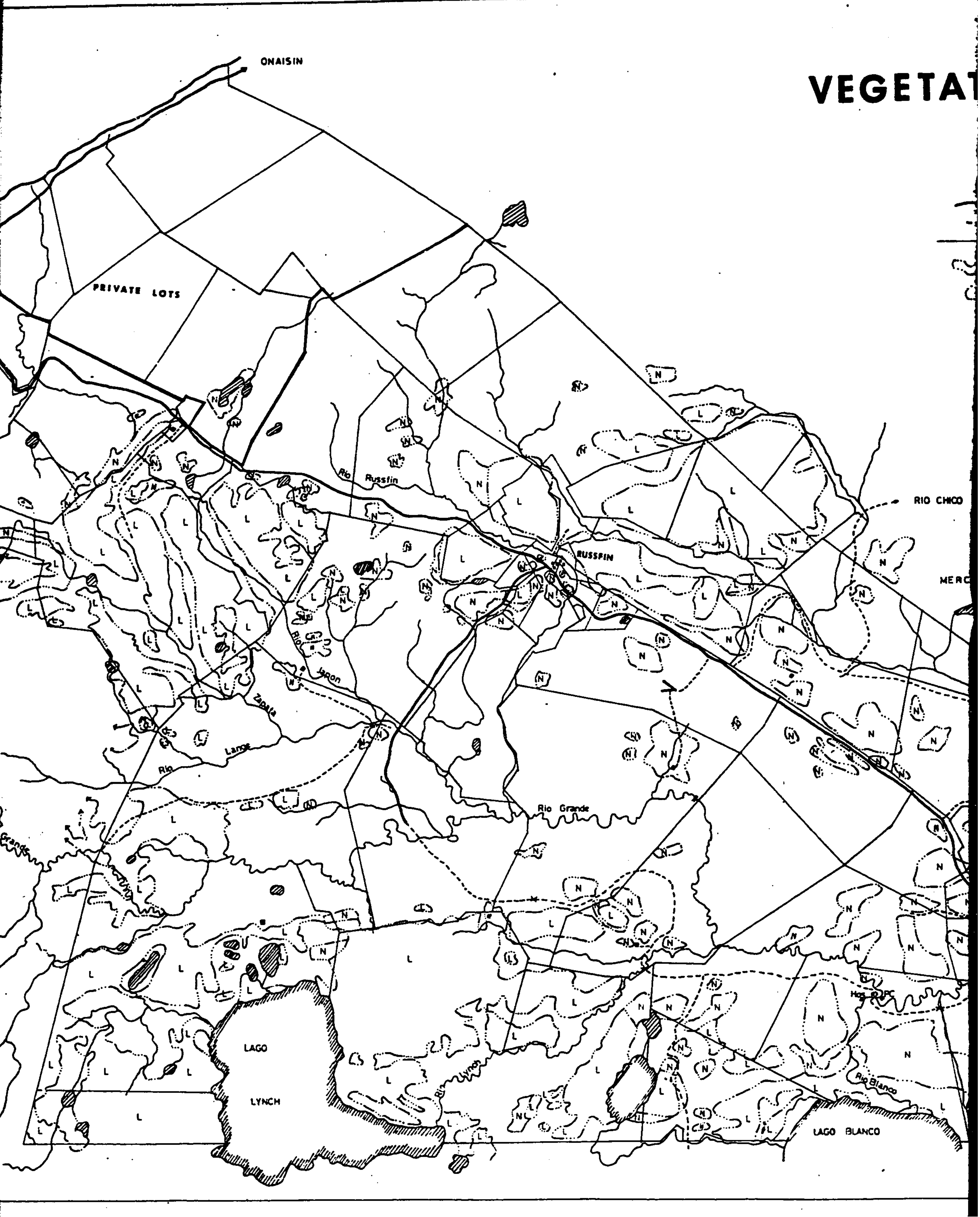
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Figure 57. Map of the stud

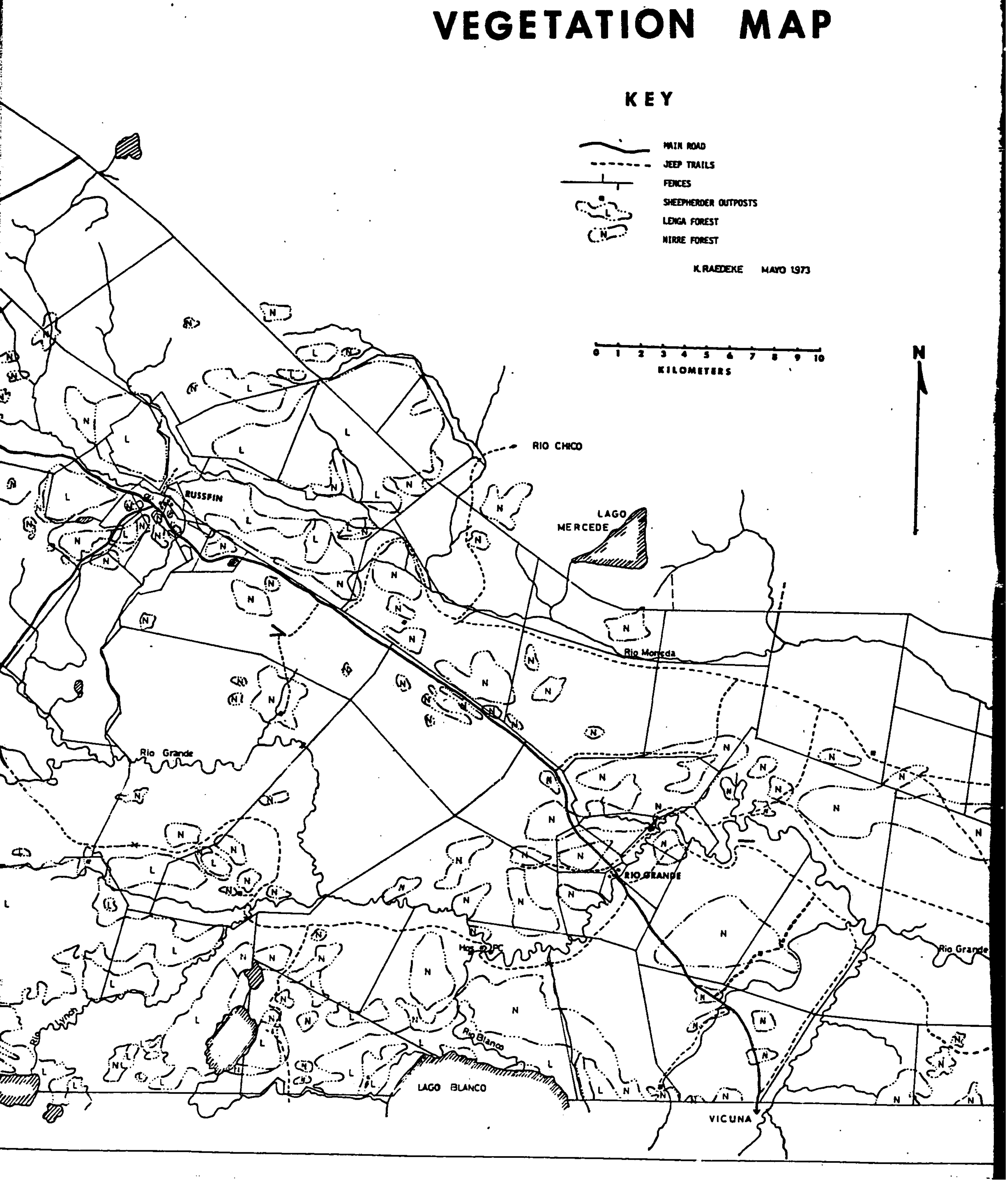
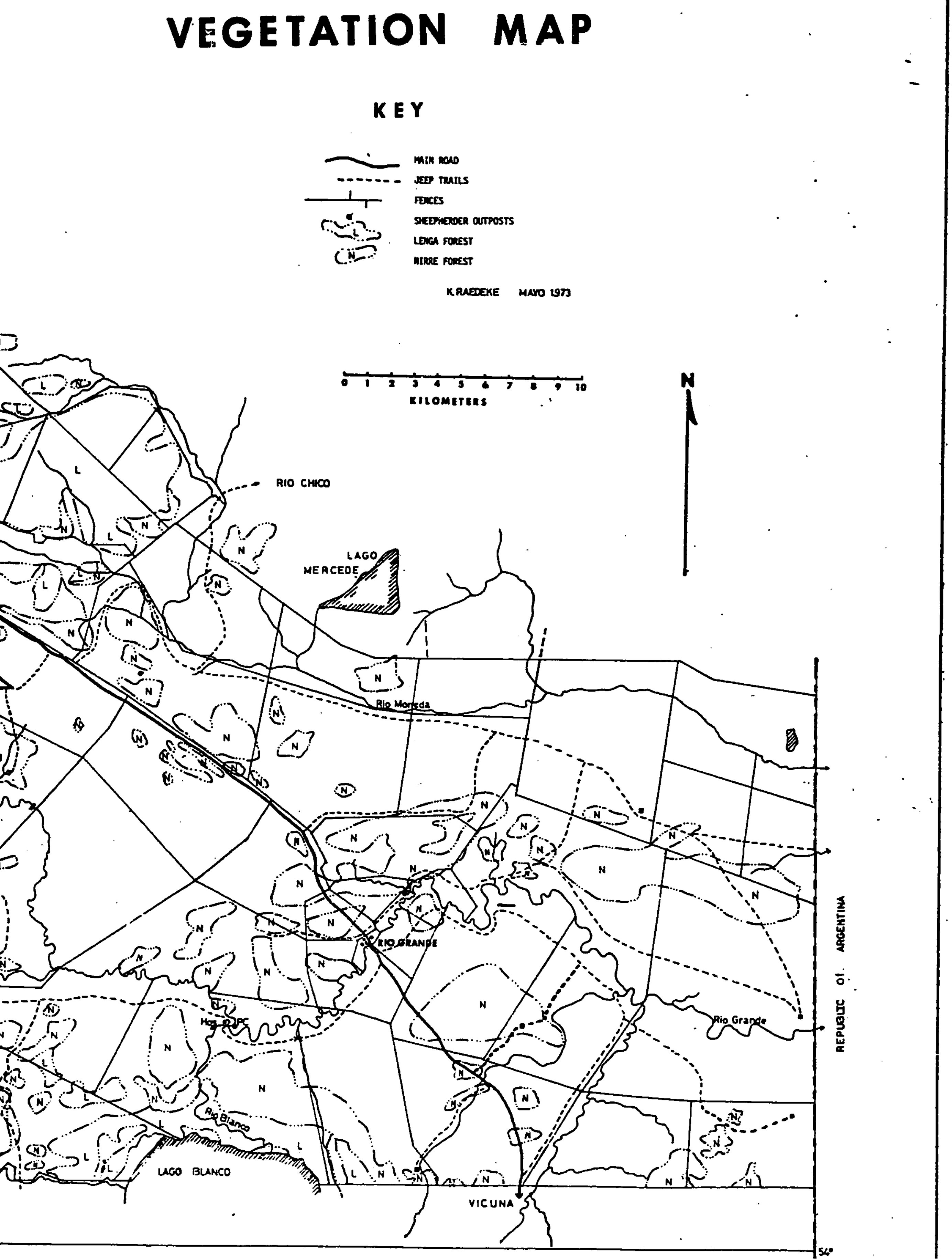
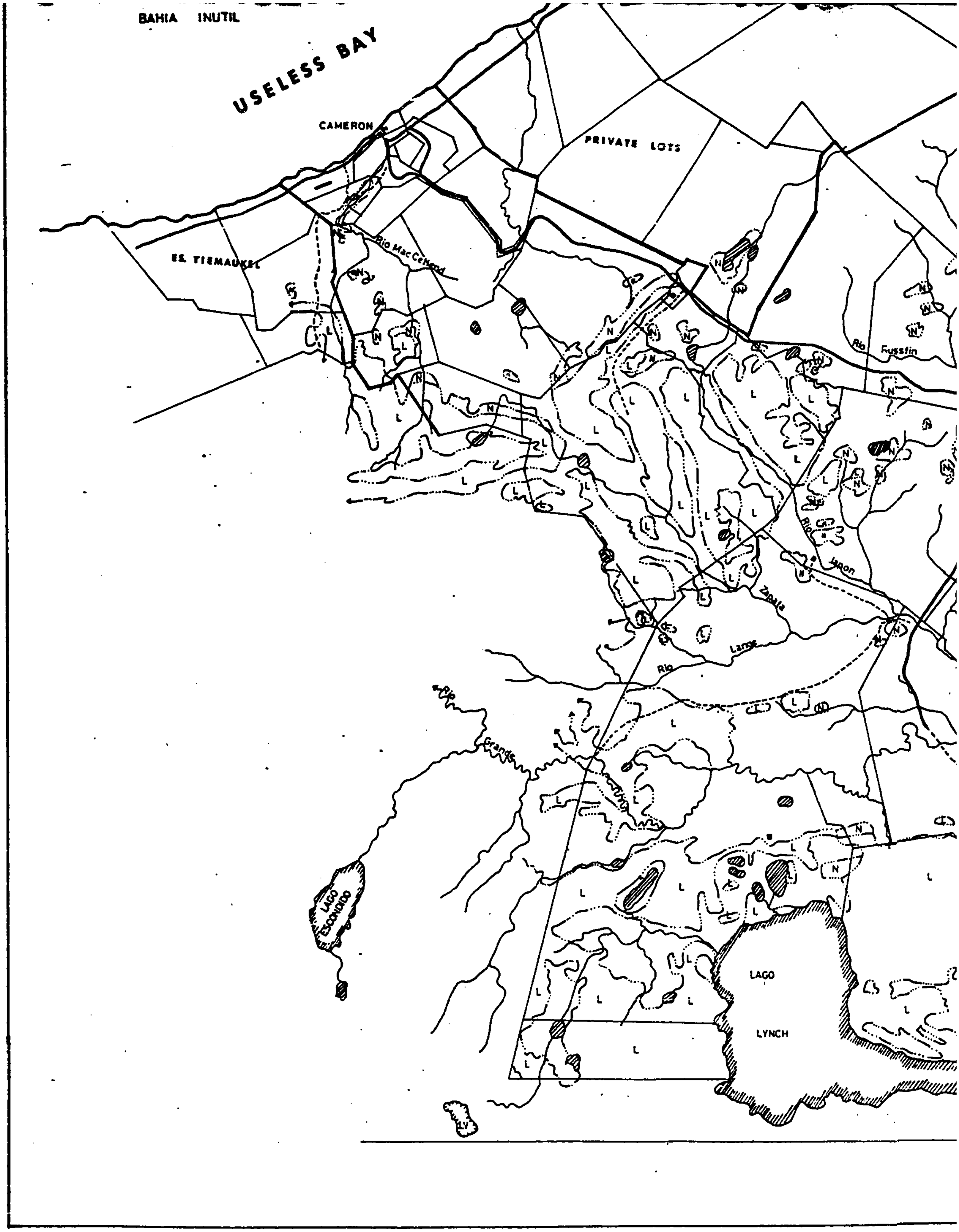


Figure 57. Map of the study area.

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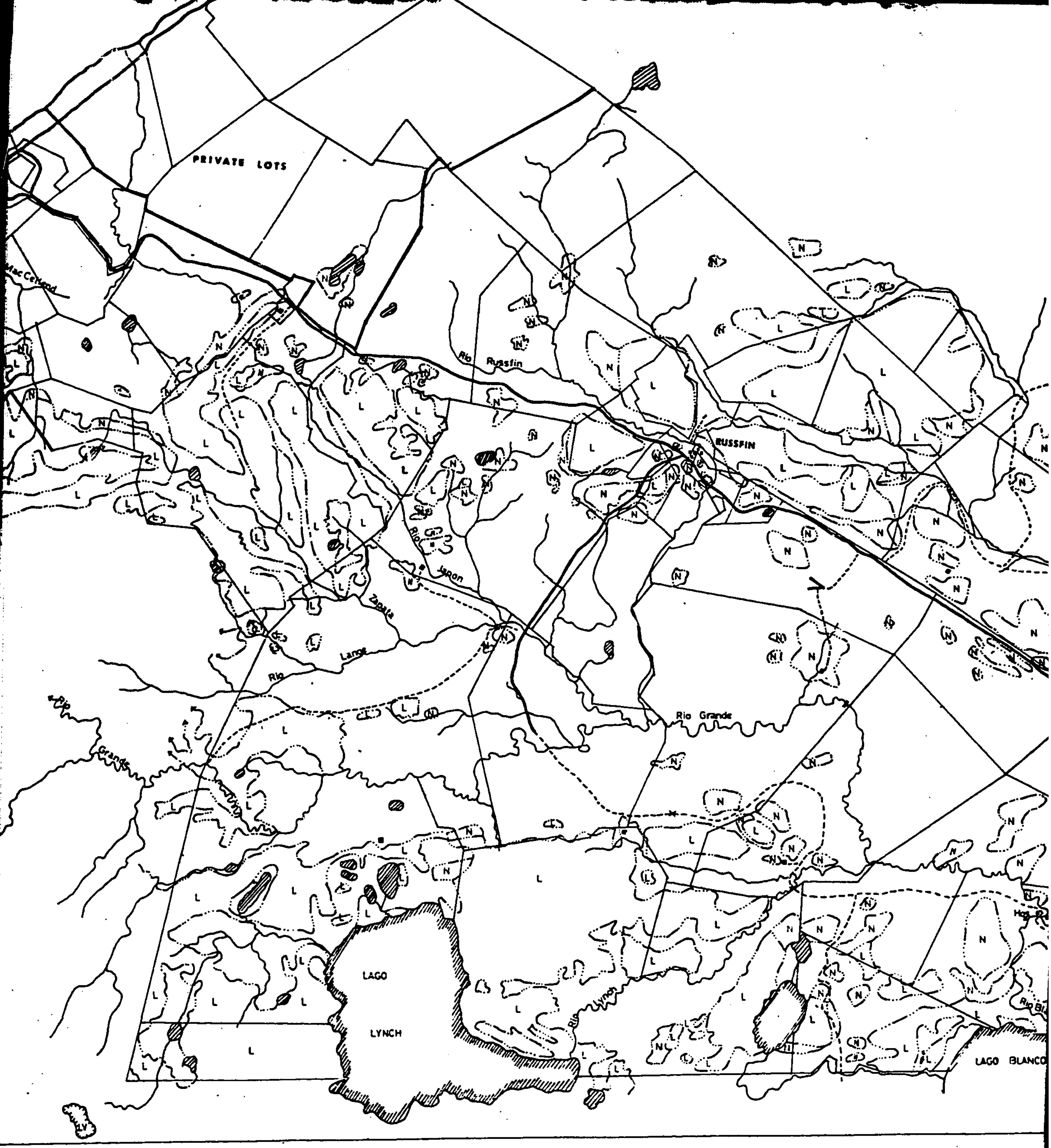
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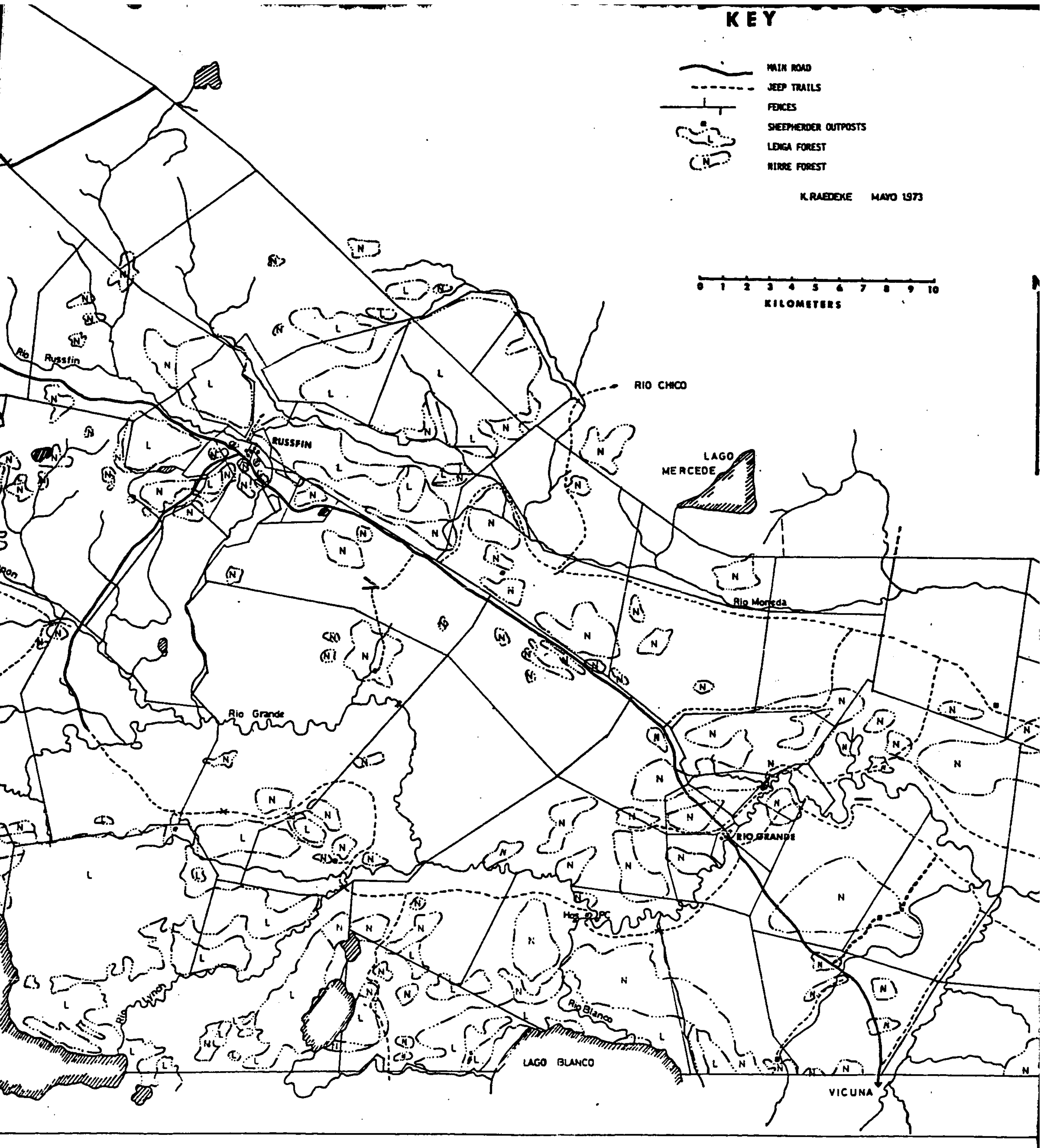
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RUSSFIN
LAGO MERCEDE
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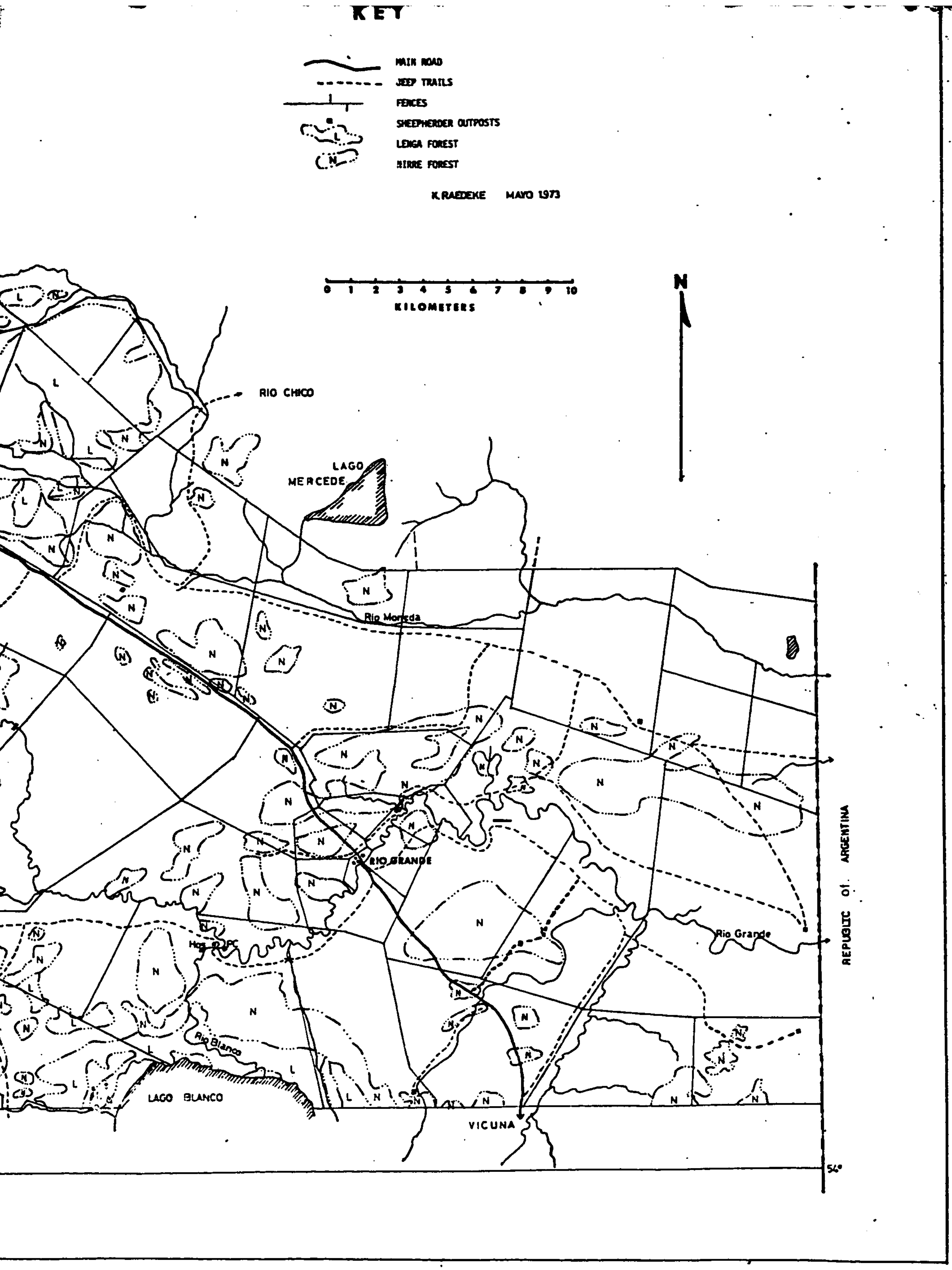
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