

HABITAT USE BY GUANACOS (*Lama guanicoe*) AND SHEEP ON COMMON RANGE,  
TIERRA DEL FUEGO, CHILE<sup>1</sup> /

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Resumen

*Se analizó el impacto de la introducción de ganado ovino en el habitat de los guanacos, comparando el nicho ambiental del guanaco antes de la introducción del ganado, con el nicho después de la misma. Se comparó el habitat autóctono del guanaco, reconstruido a partir de información literaria, con los nichos ambientales actuales tanto de las ovejas como de los guanacos, en Isla Grande, Tierra del Fuego, Chile, 1972–1975. Los modelos de empleo del habitat se determinaron mediante censos de campo de los guanacos, registros de existencia de ganado ovino, y observaciones del campo acerca del empleo del habitat por parte de ambas especies.*

*El nicho ambiental de las ovejas, en su enteridad, cabe dentro de los límites del habitat original del guanaco. Desde la introducción del ganado, el guanaco se ha encontrado desplazado de su habitat autóctono, actualmente ocupado por las ovejas que apenas dejan franjas marginales sin ocupación. Evidencias indirectas sugieren que la competencia con las ovejas eliminó al guanaco. En las áreas donde no existe ganado ovino, los guanacos manifiestan modelos de empleo del habitat similares a los de su nicho ambiental autóctono.*

Introduction

**T**he guanaco (*Lama guanicoe*) was once the most common and characteristic ungulate of temperate South America (4). However, since Darwin's time, the guanaco populations have been drastically reduced both in numbers and distribution (3, 8, 16, 19). The principal cause of the decline has been attributed to indiscriminate hunting of the guanaco for food, hides, and to eliminate the guanaco as a possible competitor with domestic stock (5). However, recent studies have shown that the factor currently most important in regulating guanaco numbers is competition with domestic stock, principally sheep, for the available forage of the range (16). This paper deals with one aspect of this compe-

tion, the patterns of habitat utilization by both species on common range. The patterns of forage utilization by sheep and guanacos have been given by Raedeke (15, 16, 17).

The interactions of sheep and guanaco populations were analyzed by comparing habitat use of both species under varying degrees of population interaction. First, the aboriginal habitat niche of the guanaco was reconstructed from published historical accounts. Second, the current habitat niches of the guanaco and sheep populations were determined from field studies of habitat use on Isla Grande, Tierra del Fuego, Chile. Third, the impacts 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.

The field studies described in this paper were conducted by the author from 1972 to 1975. This

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### The study area

All materials included in the analysis were collected from the center region of Isla Grande in the area between 69 and 70 degrees west longitude and 53 and 54 degrees south latitude. This area is within the Rio Grande river basin, at the interface of the continuous beech forest along the foot of the precordillera on the south, and the open steppe grasslands on the north. The habitat consists of a mosaic of plant communities including beech forests, matorral shrub lands, sphagnum bogs, and the steppe grasslands. The tree species include nirre (*Nothofagus antarctica*) and lenga (*Nothofagus pumilio*), both of which are deciduous. The principal shrubs are michay (*Berberis ilicifolia*), calafate (*Berberis buxifolia*), and romerillo (*Chilictrichim diffusum*). The latter shrub is a common increaser in the matorral and grassland communities. The dominant grasses are coiron (*Festuca gracillima*, *F. pallescens*, and *F. magellanica*) and various species of the genera *Stipa*, *Deschampsia*, and *Poa*. Common herbaceous plants belong to the genera *Ranunculus*, *Acaena*, *Senecio* and others. More detailed descriptions of the flora of the region are given by Auer (1), Humphrey *et al.* (6), Pisano (12, 13), and Raedeke (16).

The study area ranged in elevation from 200 to 400 meters. The topography is characterized by rolling hills and plains dissected by numerous small streams and rivers. Large lakes fill the glacier scoured valleys of the precordillera hills on the south. The entire area is grazed by sheep, domestic cattle, and horses. In 1975, the study area of 200 000 hectares supported a herd of 140 000 sheep.

The climate is characterized by cool dry summers, and rain and snow in the winters. The mean annual precipitation is 300 to 450 mm. The growing season is too short to allow cultivated crops to ripen, except in the areas with favorable microclimates.

### Methods

Habitat use by the guanacos before the introduction of sheep has been assimilated from the few

published accounts of guanaco life history, distribution, and general observations.

Current habitat use by both guanacos and sheep was determined by calculating the animal densities supported in the different habitat types in the Rio Grande river basin on Tierra del Fuego. The guanaco densities and distributions by habitat were calculated from line transect censusing and aerial surveys. The detailed methodology and results are given in Raedeke (16). The sheep densities were determined from the stocking records of the local ranches and the Chilean agricultural agencies. The distribution of range use by both guanacos and sheep within the different macrohabitats were determined by direct field observations, presented in detail in Raedeke (16).

## Results

### Original Habitat Use by Guanacos

Before the introduction of sheep, the preferred habitat of the guanaco was the open grasslands of Patagonia. The early naturalists all indicated that the highest densities of guanacos were found on the pampa (4, 14, 18, 19), especially on the fertile, moist river plains. Rogers (18) 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 regarded as secondary habitat (4).

Forested areas apparently did not support large guanaco populations. Prichard (14) 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 (9, 19), or noted only slight use of the forest habitat (3, 5). The observations of Cardozo (3) and Dennier de la Tour (5) 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 (2) was the first to suggest that the forest was adequate guanaco habitat, although inferior to the grasslands of central Isla Grande.

From these observations, it is possible to reconstruct an idealized distribution of guanacos along a vegetation ecocline. Figure 1 illustrates the reconstructed guanaco densities along the vegetation-

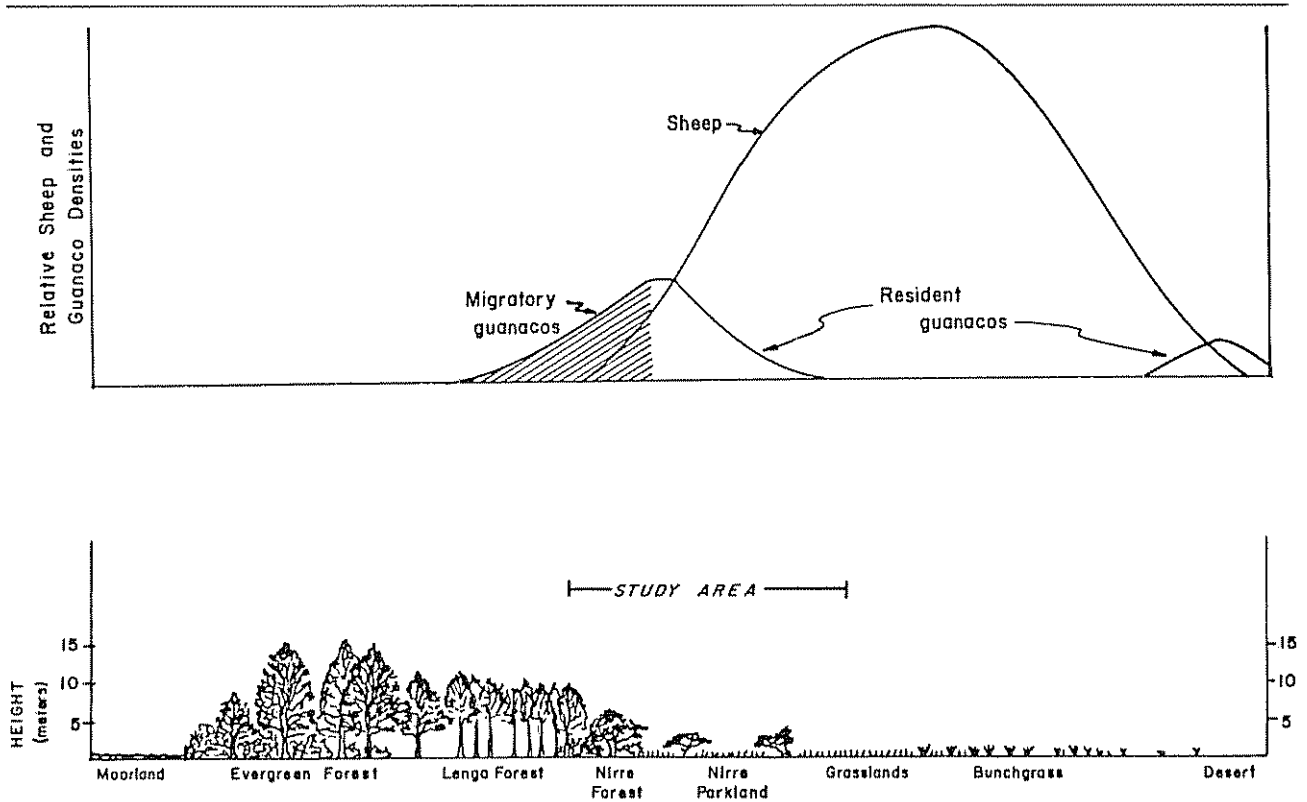


Fig. 1. Reconstructed guanaco densities along the habitat ecocline across Isla Grande, Tierra del Fuego, Chile.

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 evergreen forests and moorlands on the west side of the South American continent to the coastal deserts on the east side of the continent. The grasslands in the ecocline are equivalent to the grasslands in the Rio Grande Basin of the study area.

**Current Habitat Use by Guanacos and Sheep**

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 2, which plots the densities of the non-migratory guanacos and sheep across the pampa-forest ecocline. This figure represents the section of the ecocline in Figure 1 from the grasslands to the edge of the continuous 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. Guanacos were seldom seen more than one or two kilometers from

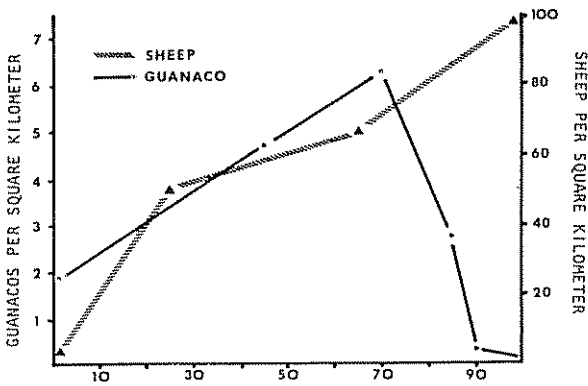


Fig. 2. Guanaco and sheep densities along the habitat ecocline in the intensive study area, Rio Grande Basin, Tierra del Fuego, Chile.

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 in the southern portion of the Rio Grande basin in Chile.

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* (21) 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.

#### Changes in Habitat Use by Guanacos Sympatric with Sheep

Both direct observation and food habits data (16, 17) indicate that when 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 proportion of the guanaco population observed 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 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 (Table 1). 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 1.6:1 in 1974. A similar shift was observed on other seasonal range types.

#### Discussion

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 1. Sheep herds have been

Table 1. Summer guanaco densities\* for forest and pampa habitats in the intensive study area, Rio Grande Basin, Tierra del Fuego, Chile (from Raedeke).

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% confidence interval.

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 1 that are east of the evergreen forest. 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.

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. In Figure 3 the idealized relative densities of the current guanaco and sheep populations are plotted along the macro-habitat ecocline, based on the results of this study. 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 1), 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 suggest that competition with introduced sheep for the range habitat and forage is the ultimate factor causing the exclusion of the guanaco from much of its former range.

First, 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 vacated sheep range in an area that had been annexed to a national park. Sheppard (20), Pianka (10), and Krebs (7) stated that the expansion of one species population subsequent to the removal of its competitor is the best evidence for competitive

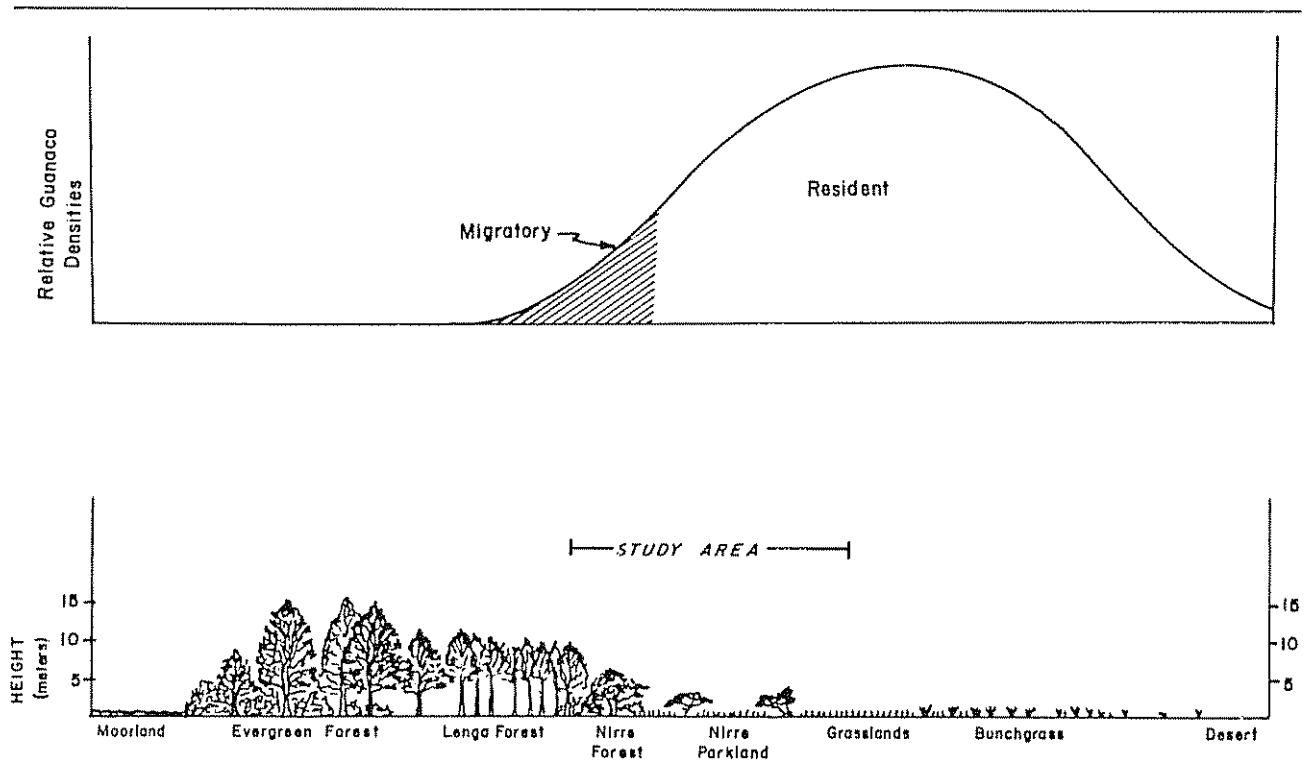


Fig. 3. The relative densities of guanacos and sheep along the habitat ecocline across Isla Grande, Tierra del Fuego, Chile.

exclusion. Pianka (11) called this phenomenon "ecological release."

Second, within the province, there are areas that are prime sheep range, but due to natural hazards, 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 (15).

Direct evidence of competitive exclusion of guanacos by sheep comes from the observation of habitat populations often thrive. The best example is the guanaco shifts with seasonal increases in sheep numbers of the study area. Guanacos shifted from heavily utilizing the open grasslands where 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 the area reduces the carrying capacity of the ranges for guanacos through nearly complete seasonal depletion of the forage. Hence, guanacos that had been displaced by sheep would face a greatly reduced survival due to a reduction of 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.

Summary

The impact of the introduction of domestic sheep on the habitat used by guanacos was analyzed through a comparison of the habitat niche of the guanaco before and after the introduction of sheep. The aboriginal habitat niche of the guanaco, reconstructed

from literature accounts, was compared to current habitat niches of both sheep and guanacos on Isla Grande, Tierra del Fuego, Chile, 1972-1975. The patterns of habitat use were determined through field censuses of guanacos, sheep stocking records, and field observations of habitat use by both species. The habitat niche of the sheep is entirely included within the original habitat niche of the guanaco. Since introduction of sheep, the guanaco has been displaced from its aboriginal habitat, now occupied by sheep, except on the fringes of the sheep distribution. Circumstantial evidence suggests that the guanacos were excluded by competition with sheep. Where sheep are not present, guanacos show habitat use patterns similar to their aboriginal habitat niche patterns.

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