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Socioecology of the Vicuna

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SOCIOECOLOGY OF THE VICUNA

by

William L. Franklin

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Science

Approved:

Major Professor	Committee Member
Committee Member	Committee Member
Committee Member	Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1976

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W. L. Franklin

William L. Franklin

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure Page

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

ABSTRACT

Socioecology of the Vicuna

by

William L. Franklin, Doctor of Philosophy

Utah State University, 1976

Major Professor: Dr. Allen W. Stokes
Department: Wildlife Science

The social organization of the vicuna (Vicugna vicugna) and its relationship to the environment were studied at the Pampa Galeras National Vicuna Reserve in southern Peru from May 1968 to April 1971. Behavioral data were collected on groups within a grid of 12.4 km^2 during 3,800 hours of observation. The vicuna's alpine grassland environment was characterized by greatly fluctuating and freezing temperatures, light precipitation, high evaporation, wind, short growing seasons, shallow and infertile soils and low plant production. Vicuna habitat quality was dependent upon high producing, preferred vegetation types and close access to permanent water and a sleeping area. Only one-third of the Reserve was good habitat and less than 20 percent of the Cupitay Valley study area was preferred by feeding vicuna. Territorial behavior has evolved in this environment where food resources are generally in short supply, annually renewed on locally abundant patchy sites, but predictable in time and space and defendable. Nearly 90 ercent of females 2 years and older were pregnant at the beginning of the birth season and 90 percent of all births occurred between 22 February and 7 April. Ten to 30 percent of the crias (juveniles) died during their first 4 months. Five social units were distinguished, with the population primarily composed of Male Groups (MGs) and family groups: Permanent Territorial Family Groups (PTFGs) occupied good habitat and Marginal Territorial Family Groups (MTFGs) secondary habitat. Most PTFGs and MTFGs each occupied a year-round feeding territory in the day and a separate sleeping territory at night. Average group size for PTFGs was six (one male, three females and two crias) and they composed about 55 percent of the population. MTFGs were smaller (five), composed 20 percent of the population, had lower reproductive success and spent less time in their feeding territories than PTFGs. Non-territorial MGs averaged 20 animals and were chased out of zones occupied by PTFGs and MTFGs. As the number of groups increased, the frequency and intensity of territorial defense by males also increased. Territories provided a place free from intraspecific interference where females could feed, sleep, mate, give birth and raise their young. Feeding territories averaged 18 ha and sleeping territories 3 ha in size. A small cluster of sleeping territories on the flattened ridge formed a cummunal sleeping area for groups using the adjacent valleys. MGs and MTFGs made greater use of ridges and the non-preferred bunch grass communities, because they were excluded from preferred areas occupied by PTFGs. Group size was significantly (P<.05) correlated with territory size and total forage production (P<.01) within feeding territories. The territorial male had a major role in the social organization of a population, since he established the location, borders and size of feeding territories. He also regulated the size of his family group by expelling the lowest ranking and youngest members before they became 1 year old (male and female crias), and by accepting or rejecting outsiders attempting to join. Marginal habitat within Cupitay Valley and vacant habitat in surrounding areas became filled by dispersing animals as the total population in the Reserve increased 36 percent during the study.

(190 pages)

INTRODUCTION

The vicuna (Vicugna vicugna) is a wild member of the South American camel family. The home environment of the vicuna is the harsh equatorial alpine short grassland, or puna. Low productivity, cold temperatures and wind characterize the treeless pampas where snow rarely falls despite the 4,000 to 4,800 m elevation.

Petrucci in 1906 (cited in Crook, 1970a) first developed the concept of social ethology when he concluded that the spatial dispersion of animals, group composition, group size and the relations between individuals were directly responsive to the environment; environmental features acting upon an animal's social system included food resources, predation and requirements for reproduction. Contemporary social ethologists focus upon three interdependent subjects (Crook, 1970a): socioecology, sociodemography and social systems research. This paper touches upon all three but is primarily concerned with the socioecology of the vicuna: the study of the vicuna's social organization and social behavior in relationship to the environment. Social organization was defined as how animals in a population are organized in space and time with respect to each other.

As a rare and endangered species with high economic potential because of its valuable wool, the vicuna has received increasing international attention since the late 1960s (Grimwood, 1969; Bate, 1968; Flowers, 1968; Hofmann, 1971; Dourojeanni, 1971; Bazán and

Ponce del Prado, 1972; Franklin, 1973a and 1973b; Winchester, 1975). Yet little is known about the vicuna's biology. Koford's (1957) excellent work from the early 1950s was the only systematic study on the ecology and behavior of the wild vicuna. His findings included qualitative observations on territorial defense, relations between and within family bands and possible functions of the vicuna territory. Much about the vicuna's biology remained unanswered. The present investigation incorporated some of these unknowns into the objectives.

The main purpose of this research was to study the social organization of the vicuna and its relationship to the environment. Specific objectives were to examine:

1. Environmental factors that could affect vicuna social organization, including the distribution, abundance, composition and production of vegetation types.

2. How males establish and maintain their territories and how this might affect use of habitat resources.

3. The relationship between resources within a territory and size of the territory and family unit.

4. If there might be any effects of social organization upon regulation of population size.

METHODS

Behavioral Observations

A grid of 12.4 km^2 was laid out in Cupitay Valley on the northern edge of Pampa Galeras Reserve (Figure 1). The grid covered a 4.2 km length of the valley floor, the north and south-facing slopes and the southern ridge. Rock cairns 1 m in height were spaced 200 m apart in lines at right angles to a straight road.

Four observation huts were constructed on high vantage points within the gridded study area (Figure 1). By means of the cairns, one could estimate and record locations within the grid to the nearest 20 m. Zone I (4.26 km^2) included the area that could be readily observed from one observation hut and Zone II (2.90 km^2) from a second observation hut. A small area (0.38 km^2) that could be observed from both huts is shown in Figure 1. Once every hour the area was scanned from left to right, and the following information about each vicuna group present was recorded on a map of the study area: total number of animals, composition of group, location, number of adults and crias (young less than 1 year old) feeding and the vegetation type being consumed. Ten to 20 groups were typically under observation at the same time. Details of intergroup aggressive encounters (territorial defense) were recorded throughout the hour. As groups left the observation zone and moved onto the adjacent ridges in the afternoon, they were no longer visible. Recordings of the location, numbers and types of domestic livestock in the observation zone were also made hourly. Disturbed movements of vicuna groups due

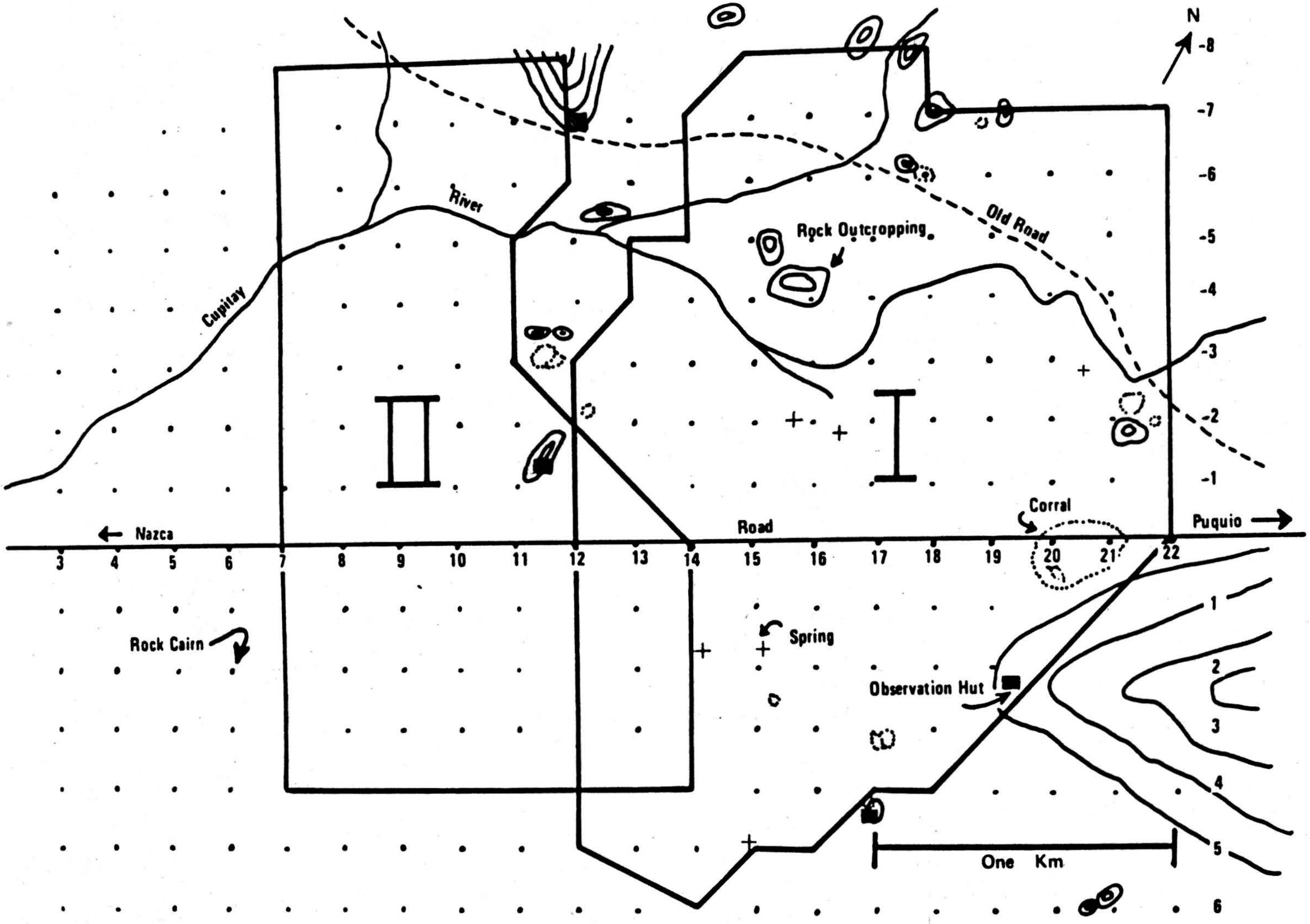

Figure 1. Cupitay Valley study area showing observation huts, grid, Zones I and II and major land features.

to activities of people, livestock and dogs were recorded. By the end of a day a group's continuous route of movement was obtained through these hourly samples. Qualitative notes were taken on unusual events such as changes in group composition, fighting, births, matings and predation.

The above observations were made for 27 months from February 1969 to April 1971. Observations were started at sunrise. Two observers recorded intergroup information until noon, at which time a third observer replaced them both and remained until dark. If it was not possible to observe the entire day, observations were made only in the morning.

A total of 3,623 hours of observations were made from March 1969 to April 1971 (2,209 hours in the morning and 1,414 hours in the afternoon), of which 56 percent were in Zone I and 28 percent in Zone II. Hours observed per month varied from 36 to 227 and averaged 134. The seasons were divided into 3-month periods, beginning with fall on 1 May. Year One was from 1 May 1969 to 30 April 1970 and Year Two, 1 May 1970 to 30 April 1971.

Complete counts were made of vicuna within the Pampa Galeras National Vicuna Reserve in August 1968 and during a return visit in December 1971. Each census was conducted over a 3-day period from midmorning to late afternoon with the help of 2 or 3 assistants. These counts included the study area south of the Nazca-Puquio road and not those parts of Zones I and II north of the road. Monthly and seasonal population densities within the study area were based upon the mean number of animals observed per hourly scan divided by the surface area of the zone under observation.

Vicuna Units (V.U.) were used to equate animals of differing sizes when calculating habitat utilization, feeding use and preference for vegetation types. Adults and yearlings were each considered full Vicuna Units. Crias were rated by age: <3 months old (March, April, May) = 0.2 V.U.; >3 but <6 months (June, July, August) = 0.4 V.U.; >6 but <9 months (September, October, November) = 0.6 V.U.; >9 but <12 months (December, January, February) = 0.8 V.U.

Preference indices were computed for vicuna feeding on the different vegetation types. To do this the percentage of total vicuna observed feeding on a vegetation type was divided by the percentage of the total hectares that type represented in the study area and multiplied by 100. A preference index of more than 100 indicated vicuna spent relatively more time feeding on a particular vegetation type than would be expected from that type's availability.

An intensive study of family group 211 was made from August 1970 to January 1971 totaling 142 hours. Nearly all observations were made between 0600 and 1200 hours. Detailed data were taken on all defecations and urinations, the male's behavior during intergroup encounters and aggression within the group. Samples were made of aggressive encounters 20 minutes each hour for a total of 45 hours.

During 1970 and 1971 six crias were hand captured, ear tagged and released. Crias could be run down on foot only within the first 15 minutes after birth. For those groups without tagged animals or without individuals recognized by natural markings or defects, identification was based upon group composition and consistent use of the same site.

The sex of a vicuna is difficult to determine in the field because males and females lack obvious sexual dimorphism. An individual could be sexed when it raised its tail during defecation, revealing the absence or presence of testes. Both sexes urinated posteriorly with the hindlegs parted and the hindquarters dropped slightly, but the male's urine was at the level of the hocks, while the female's urine originated at the level of the tail. The small dark and hairless penis on males and the udder on lactating females were occasionally visible too. Free-ranging adult males and females could also be distinguished by behavioral differences. Adult females were nearly always with a family group; if not, solo females were usually not aggressive when attempting to enter a family group, showed no interest in other adult females, were treated less aggressively by territorial males and did not defend a site as did males. Yearlings were distinguished by their smaller bodies, wool of less uniform length and more shaggy in appearance and shorter muzzles than adults.

Environmental Measurements

Fifteen vegetation types were identified in the study area and were analyzed by the point frame method as described by NAS-NRC (1962). The point frame was 110 cm long with the 10 pins spaced 10 cm apart. A homogeneous stand of each vegetation type was chosen by its characteristics of visual uniformity. A line transect was selected through the type and a minimum of 10 stops (100 pin drops) were made per line. During the last month of the 1970 growing season (April), 13 vegetation types were analyzed with 16,100 pin-drops.

A vegetation type map of 431 ha with a scale of 20 m to 1 cm was made by ground reconnaissance from atop high peaks and ridges using binoculars and spotting scope. The vegetation types within each 4 ha section were drawn in proportion to their size and distribution.

Plant production of each important vegetation type was estimated by clipping plots where ungulate grazing had been excluded by wire cage exclosures during the 1970 and 1971 growing seasons. The term production refers to the amount of dry plant material produced per unit surface area per year. Each year cages were put out in January before the growing season began. Cages were placed on sites judged to be quantitatively and qualitatively representative of the type. At the end of each year's growing season, the forage within 1 m^2 plots was clipped to ground level from inside 1.2 m^2 cages, oven dried and weighed. For shrubs and tall-coarse grasses only the current year's growth was clipped.

Total production within territories was estimated by multiplying the total surface area of each vegetation type within the territory by the mean production for that type. Plant species not used by vicunas, namely the large unpalatable bunch grasses, were not included in these estimates of total available food resources within a territory. In August 1970, 39 unprotected (grazed) 1 m^2 plots were clipped to estimate forage utilization. Each was paired with a protected plot within 10 m. Both plots had visually the same plant composition. A total of 132 soil pits were dug in 11 different vegetation types to measure the mean depth of soil horizons A_1 and A_2.

Weather data were obtained from the climatological station at the Pampa Galeras headquarters 2.5 km west of the study area. Standardized weather information was taken daily at 0700, 1300 and 1900 hours. Climatological information was averaged by 2-week periods beginning with August for each annual cycle. Thermometers in standard weather houses placed on the ground measured maximum and minimum temperatures in the study area.

RESULTS

Description of the Study Area

This investigation was made at the Pampa Galeras National Vicuna Reserve in southern Peru's department of Ayacucho (14°40'S, 74°25'W), 450 km south of Lima. Established in 1966 by the Ministry of Agriculture's Directory of Forestry and Wildlife, Pampa Galeras was the world's first vicuna reserve. The Reserve has greatly contributed towards saving the vicuna from near extinction. The field research was conducted from May 1968 to April 1971.

The 6,500 ha Pampa Galeras Reserve lies on the western edge of the Andean altiplano plateau at 4,000 to 4,300 m elevation. This treeless alpine grassland is characterized by broad open valleys separated by flattened ridges (Figures 2a and 2b). Precipitation occurs mainly in the summer. Nightly temperatures almost always are below freezing. Plant formations are primarily Subalpine Scrub Desert and Humid Alpine Tundra, with some areas of Subalpine Humid Puna and Very Humid Alpine Tundra (Tosi, 1960).

A knowledge of the vicuna's environment is necessary to understand its behavior and social organization. Climate, distribution of water, plant communities and forage production might all affect the spacing of vicuna social groups, habitat use and preference, and the distribution and size of territories.

Figure 2a. Pampa Galeras National Vicuna Reserve, Peru.

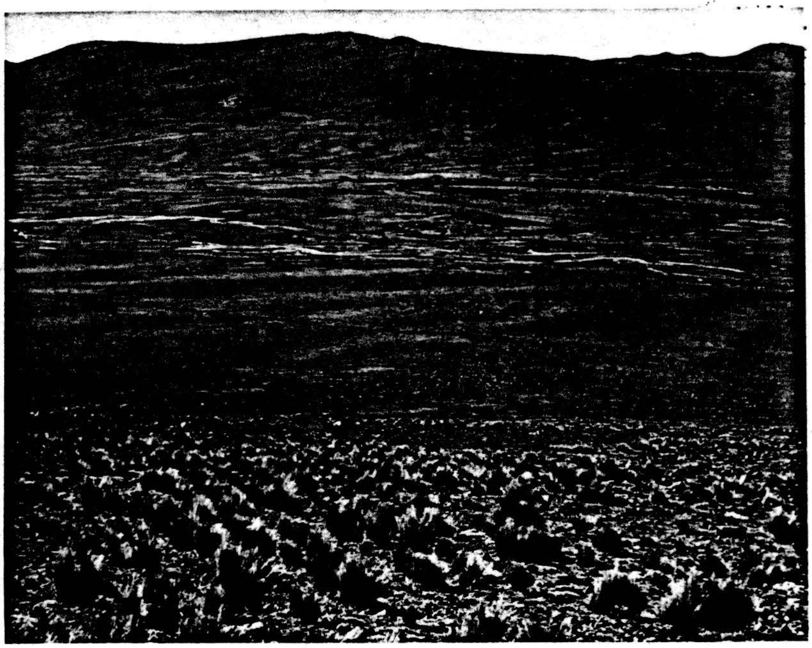

Figure 2b. Cupitay Valley study area.

Climate

Two general climatological periods occur in this part of the Andes: a mildly warm, rainy growing period from December through April and a cold, dry period from May through November. The fall (May, June and July) is characterized by freezing nights, cool days, no rain and drying vegetation; the winter (August, September and October) by freezing nights, cool days, little rain and dry and dormant vegetation; the spring (November, December and January) by a decrease in the number of freezing nights, cool days, an increase in precipitation and some plant growth; and the summer (February, March and April) by cold nights, cool to mild days, almost daily precipitation and plant growth.

The mean annual precipitation in Pampa Galeras for the 5 years 1967 to 1971 was 487 mm and varied from 281 mm to 742 mm. During these years, 90 percent of the annual precipitation came during spring and summer and 81 percent from December through March. The mornings in the rainy season were clear, warm and rainless until noon, when storm clouds came from the east. Precipitation was usually in the form of hail or rain but rarely snow.

Mean annual temperatures for 1968 through 1971 were 4.6°C, 5.0°C, 5.3°C and 5.5°C. From 1967 to 1971 mean minimum and mean maximum temperatures for fall were -5.1°C and 12.2°C; for winter, -4.6°C and 13.4°C; for spring, -1.3°C and 12.9°C; and for summer, 0.5°C and 12.4°C. The nightly average minimum temperature was below freezing year-round except during a few weeks in late spring and summer (Figure 3).

Cloud cover from late spring and summer storms had a profound effect upon the nighttime minimal temperatures, which in turn appeared to affect the length of the growing season and, ultimately, plant production. Nocturnal cloud cover maintained night temperatures above freezing. For example, in the summer of 1967, clouds covered 75 to 100 percent of the sky 75 percent of the time; the mean minimal temperature for this period was 1.7°C. In contrast, during the fall of 1967 when daily maximum temperatures averaged the same as summer, the cloud cover was only 0 to 25 percent 71 percent of the time and the mean minimum temperature was -4.7°C (Figure 4). Lapses of cloud cover in midsummer caused nighttime minima to drop below freezing.

The number of frost-free weeks when plant growth occurred varied from 8 to 17, averaging 13 from 1967 through 1971 and appeared to have a close relationship with plant production. In 1970 the growing season was 17 weeks long. In 1971 it decreased to only 8 weeks and total production declined 40 percent.

The growth season at this high altitude was not necessarily "a period when sufficient moisture permitted the growth of the existing natural vegetation" (ONERN, 1971), but a period when sufficient nighttime cloud cover maintained the nightly minima above freezing. Thus, total annual precipitation reflected, but did not fully control, the length of the growing season. Total precipitation in

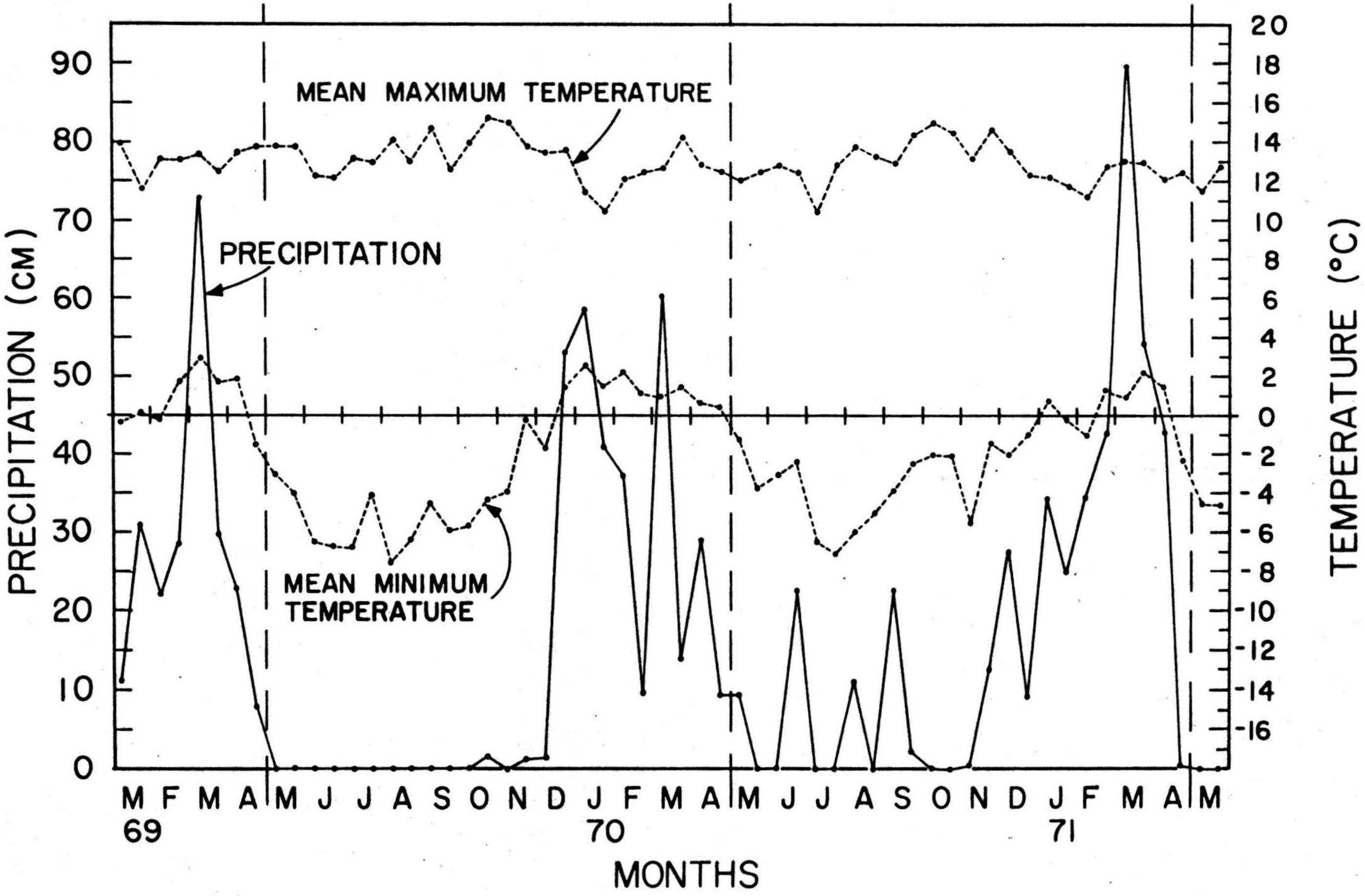

Figure 3. Relationship between precipitation, mean minimum temperatures, and mean maximum temperatures in Pampa Galeras Reserve, January 1969 to May 1971.

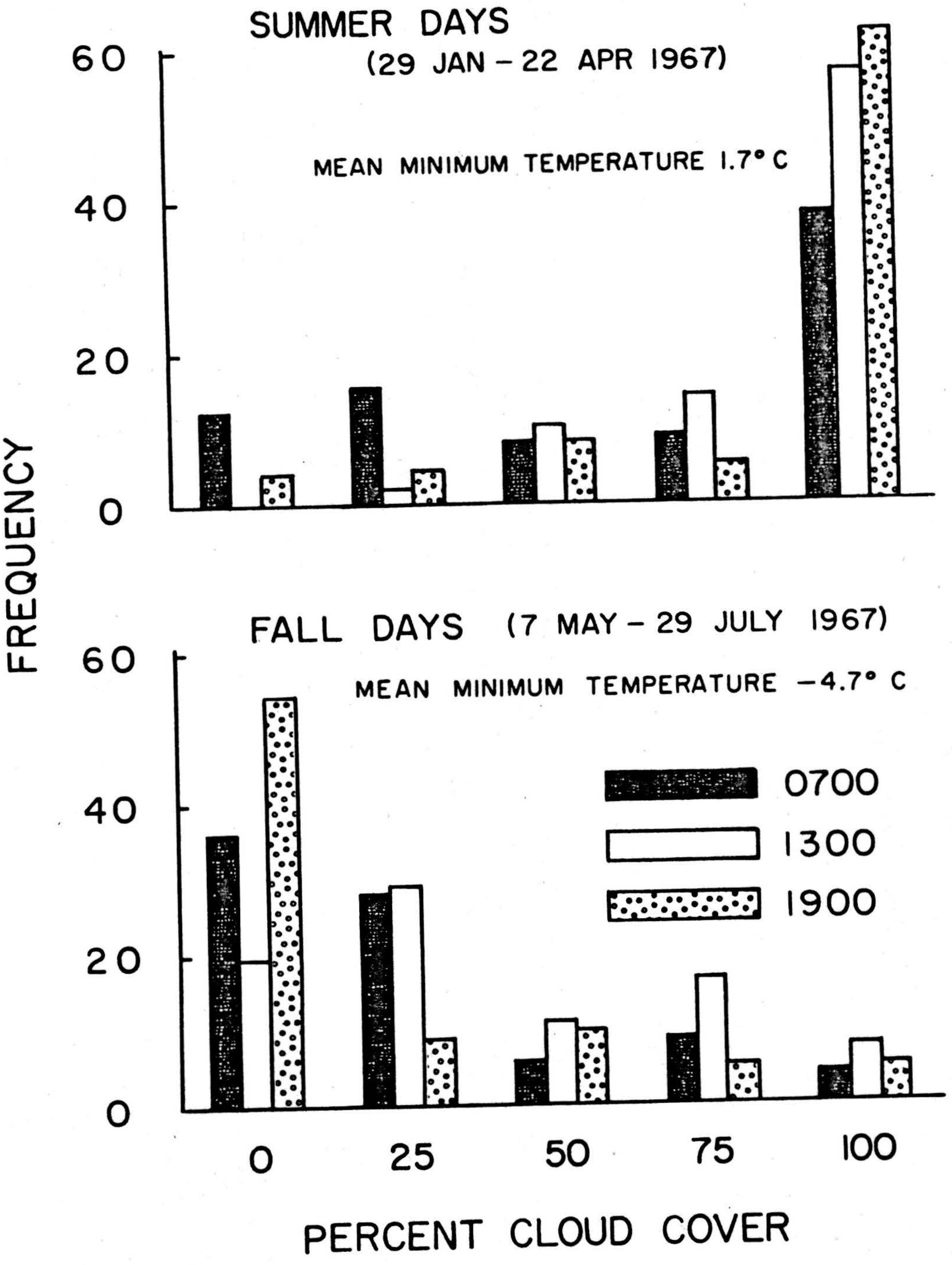

Figure 4. Relationship between cloud cover and mean minimum temperature for summer and fall days. Observations were made three times per day on 83 days during each season.

1971 was 70 mm greater than 1970, yet the 1971 growing season was less than half as long as that of 1970. An unusually "wet" dry season occurred in 1971 when much of the annual moisture fell in fall, winter and early spring; however, cloud cover from these storms was not sufficient to bring the nightly minima above freezing (Figure 3).

Differences in minimum and maximum temperatures within the Cupitay Valley study area were measured for the ridge (sleeping area), slope, flat and bottomland during August 1970. Daytime mean maxima ranged from 17.1°C to 19.0°C; the ridge was the coolest of all locations. Nightly mean minima ranged from -3.3°C to -11.0°C. Temperatures on the bottomland averaged nearly 7°C colder than on the ridge sleeping area, although the ridge was only 18 to 20 m higher than the bottomland in elevation.

Topography and distribution of water

Elevation in the Cupitay Valley study area ranged from 4,059 m on the level bottomland at the center of the valley to 4,077 m on the ridge. The area between the bottomland and the road was referred to as the flat, while the area between the ridge and flat was called the slope (Figure 5).

Figure 5 gives the locations of surface water in the bottomland associated with the Cupitay River and of springs on the flat and slope that contained water during the first half of the dry season. By late winter, most springs had either dried up or were insufficient to satisfy the needs of vicuna.

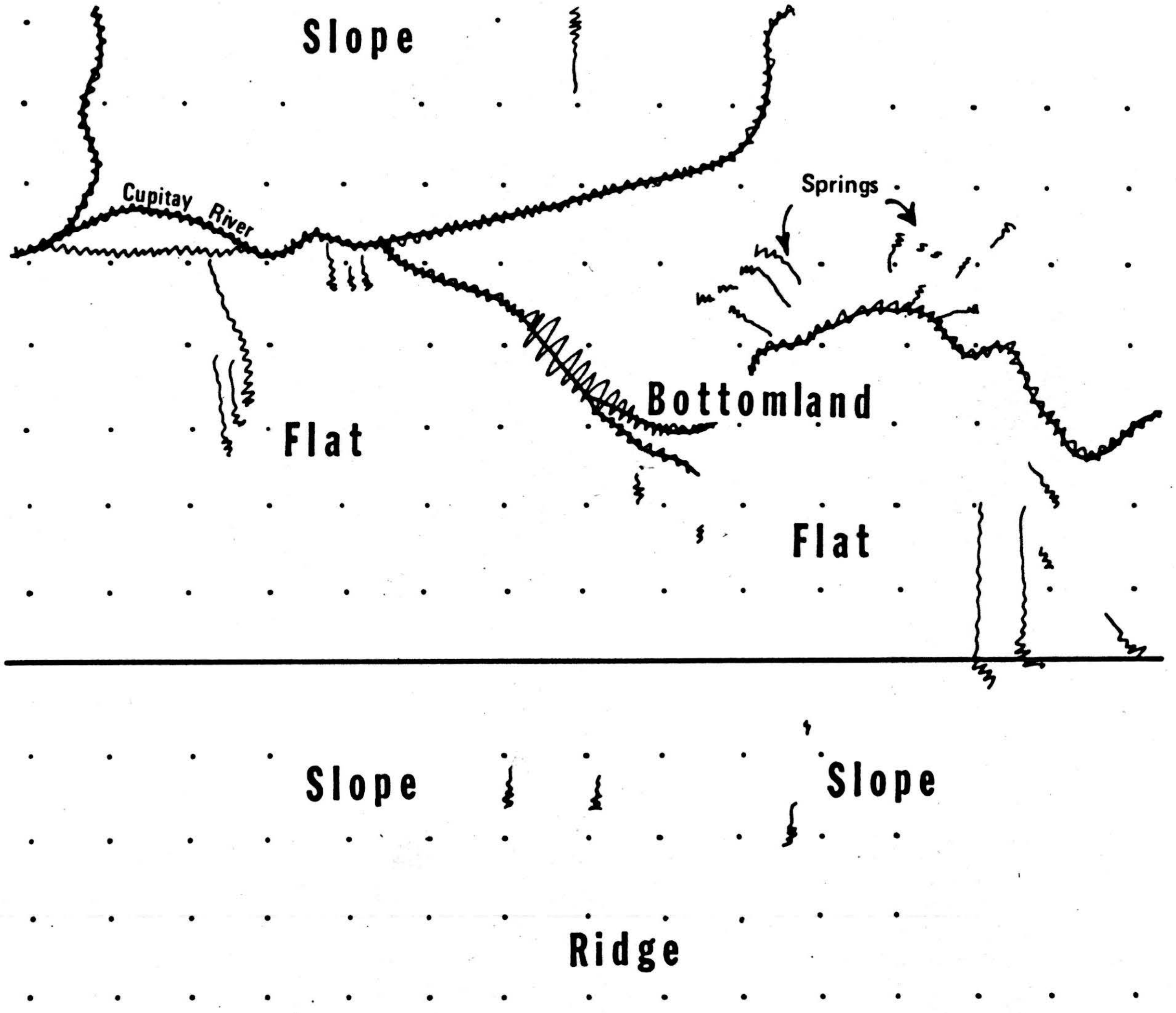

Figure 5. Distribution of surface water during June and July, 1970, Cupitay Valley study area.

Vegetation types

Information on plant species composition, topsoil depth and production of vegetation types (VT) is given in Table 1. Points of special interest on selected VTs for helping understand the socio-ecology of the vicuna are presented below. The types are given in order of abundance.

VT-2 was the most common plant community. It was the dominant type on the flats and lower slopes, but was also common on the ridges. VT-2 was easily recognized by its abundance of surface rocks of igneous origin and by the sparsity of plants (Figure 6). Plant production per hectare was low and feeding vicuna showed no preference for this type.

VT-11 was dominated by *Festuca dolichophylla*, a tall-coarse and unpalatable bunch grass (Figure 7). This type was common on the upper dry slopes occurring as large units throughout the Reserve. VT-11 ranked second highest in production per hectare in 1970, but was the least preferred of all vegetation types (Figure 8). Nearly 75 percent of the production was from *Festuca dolichophylla* in 1970.

VT-4 occurred on the flats as irregularly shaped patches or on the slopes as linear downhill lines. This type was dominated by another large-coarse and unpalatable bunch grass, *Stipa ichu* (Figure 9). Sixty percent of the production in VT-4 was from *Stipa ichu* in 1970. Vicunas showed no feeding preference for VT-4. Vicunas fed on the small understory plants in VT-4 and VT-11 and not the large-coarse bunch grasses. In fact, vicunas rarely fed on bunch grasses

Table 1. Characteristics of vegetation types found in Cupitay Valley study area, Pampa Galeras National Vicuna Reserve, Peru. Total surface area of vegetation types equals 669.3 ha. List of species includes those that contributed greater than 2 percent relative cover.

	VEGETATION TYPES												
	2	11	4	3	1	13	12	6	7	10	14	8	15
COMMON NAME	Roqueño	Ichu	Peccoy	Chiula	Quisna	Taxona	Quisna Sin Influencia	Mojadal	Pampa Verde	Piedras De La Loma	Chiula General	Pampa Verde Claro	Pampa Verde Obscuro
RELATIVE SURFACE AREA	48.1%	15.5%	13.5%	6.4%	5.3%	2.5%	2.1%	1.7%	1.4%	1.3%	0.6%	0.5%	0.2%
TOPSOIL DEPTH (CM)	16.6	16.0	18.6	22.8	23.8	19.5	20.5	25.3	-	11.5	24.0	24.3	-
(N= number of soil pits)	(43)	(11)	(16)	(12)	(32)	(4)	(2)	(4)	-	(2)	(3)	(3)	-
PRODUCTION (KG/HA)													
1970	490	1390	1250	920	1550	480	410	660	580	530	770	500	960
(N= number of $1m^2$ plots)	(13)	(2)	(4)	(8)	(12)	(5)	(2)	(4)	(1)	(1)	(2)	(2)	(1)
1971	320	960	800	310	620	230	320	-	-	490	280	200	-
(N= number of $1m^2$ plots)	(11)	(3)	(2)	(8)	(10)	(4)	(2)	-	-	(1)	(2)	(2)	-
ABSOLUTE PERCENT COVER													
Plants	59.4%	65.0%	81.7%	83.6%	92.3%	79.6%	92.0%	75.7%	99.0%	35.0%	85.0%	86.2%	97.0%
Bare Ground	18.4	16.9	10.4	7.3	5.5	12.3	8.0	24.3	1.0	21.0	5.7	13.8	3.0
Surface Rocks	22.2	18.1	7.9	9.1	2.2	8.1	0.0	0.0	0.0	44.0	9.3	0.0	0.0
(N= # of point-frame pins)	4100	1000	2100	2100	3600	700	100	300	100	200	300	400	100
RELATIVE PERCENT PLANT COVER													
Tall And Unplatable Coarse Grasses													
Festuca dolichophylla		28.3											
Stipa ichu		3.3	25.7										
Short And Palatable Grasses And Grasslikes													
Perennials													
Festuca rigesens	4.8			19.4		7.5	3.4				14.8		
Poa aequigluma							6,8						
Poa "galeras"	13.6	8.8	2.6	2.9	4.1	12.0				5.3		4.4	
Poa sp. 2					2.7								
Calamagrostis vicunarum	2.8		3.7	5.2	19.1	8.2	13.7			4.4	3.7	14.4	
Calamagrostis heterophylla		3.3										2.7	
Calamagrostis jamesonii									8.8				8.7
Calamagrostis trichophylla										3.5			
Muhlenbergia ligularis							4.1				2.7		
Stipa brachyphylla										8.9			
Stipa depauperata	8.2	10.0	3.8	5.5	2.1	5.9					6.0		
Stipa sp. 6										15.0			
Aciahcne pulvinata						4.7						8.5	
Gramineae sp. 1								5.5					

Table 1. Continued.

	VEGETATION TYPES												
	2	11	4	3	1	13	12	6	7	10	14	8	15
Annuals													
Dissanthelium minimum			6.5		4.1								
Muhlenbergia peruviana	28.6	21.2	27.5	10.3	14.4	9.8	19.9			33.6	16.4	4.4	
Cyperaceae sp. 1	6.4	3.8	11.4	5.2	6.1	3.9					8.0	6.6	
Forbs													
Isoetes af. hieronymi				2.3			8.9				3.7	3.6	
Malvastrum sp. 1					2.8						3.1		
Nototriche sp. 1					2.3							3.2	
Arenaria tetragyna					9.2								
Alchemilla pinnata			2.2	8.3	12.7	7.7	8.2				7.2	14.6	
Trifolium amabile		2.2	2.0	2.6							4.9		
Compositae sp. 1	3.2	3.0	2.0							4.4			
Compositae sp. 2								3.2					
Hypochoeris taraxacoides							2.1						
Werneria pygmaea	4.3			6.4	2.3	3.5	6.2		12.6		5.3	12.9	22.8
Eleocharis sp.				3.9	4.4		19.2		14.8		4.3	4.4	23.9
Shrubs													
Baccharis tricuneata		2.6								4.4			
Senecio spinosus	3.6	2.8								6.2			
Tetraglochin strictus										2.7			
Cushion Plants													
Caryophyllaceae sp. 1								48.1	30.2				18.5
Pycnophyllum molles										3.5			
Pycnophyllum sp. 2				2.2		18.3						2.5	
Azorella diapensiodes	3.6			4.0		3.9					4.3		
Plantago rigida								23.2	33.0				17.4
Disticha muscoides								7.8					
Miscellaneous													
"Recto" sp.								3.7					
"Vacio" sp.								2.9					
"Bareo" sp.													8.7
Unknown sp. 11				3.6			2.1						
Unknown sp. 16				4.7	3.6						7.0		
Unknown sp. 17											2.2	3.1	

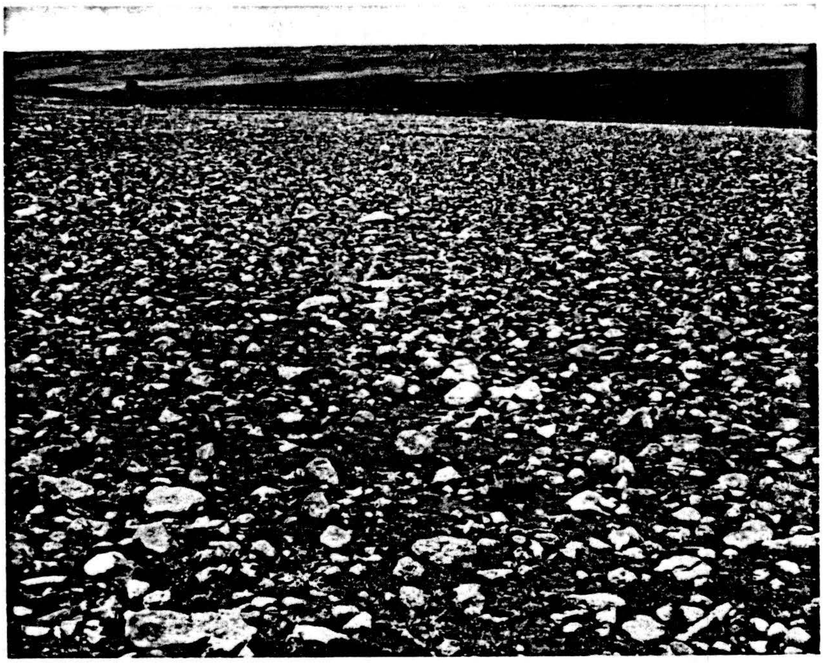

Figure 6. Vegetation type-2 dominated by surface rock, Muhlenbergia peruviana and Poa galeras. This was the most common plant community.

Figure 7. Vegetation type-11 dominated by the unpalatable Festuca dolichophylla.

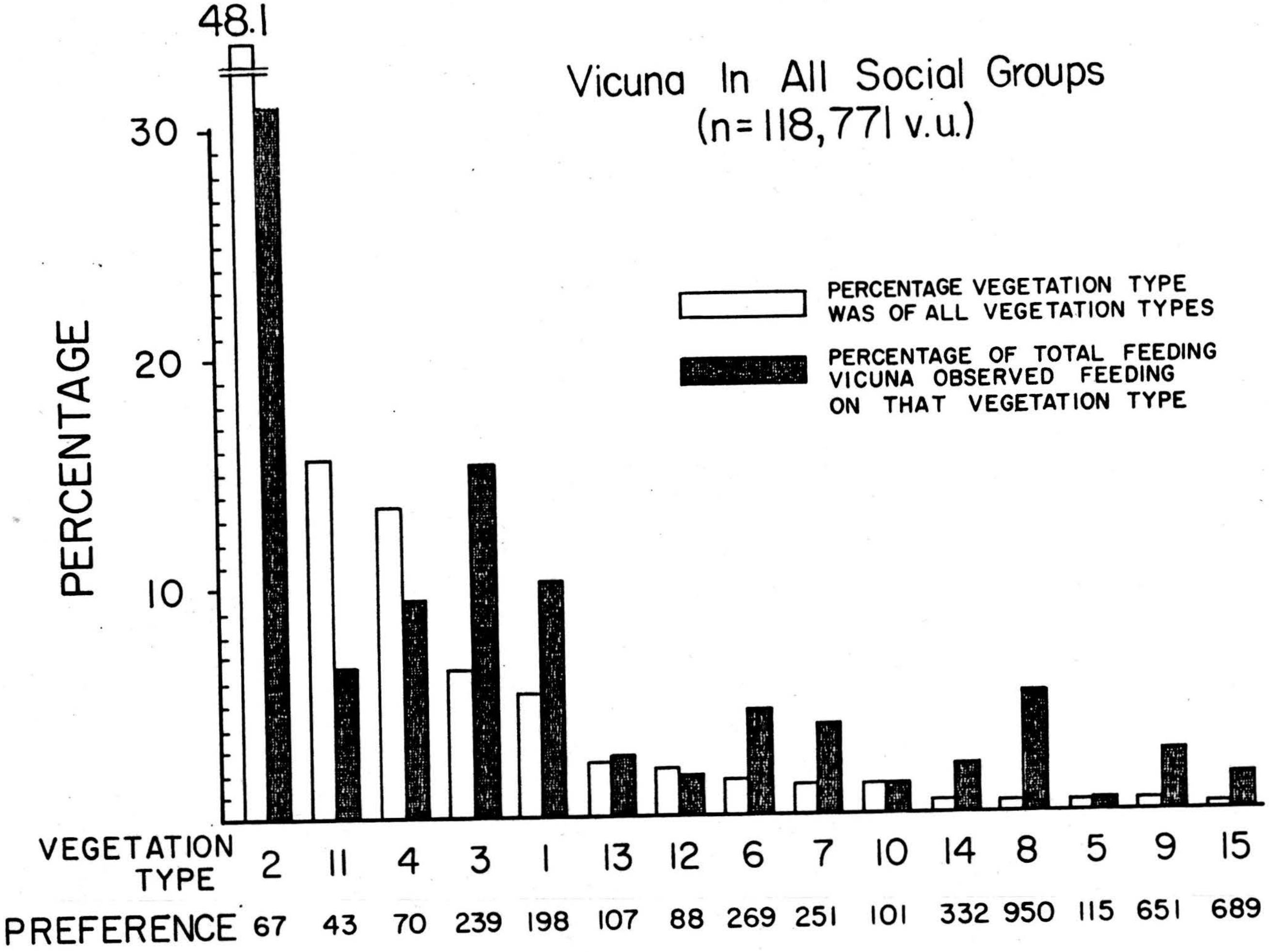

Figure 8. Feeding use and preference for vegetation types by all vicuna.

Figure 9. Vegetation type-4 was dominated by the large and unpalatable Stipa ichu. This type occurred in large patches on the flat and in downhill lines on the slope.

Figure 10. The highly preferred vegetation type-3 was dominated by Festuca rigesens.

or shrubs but were strictly grazers on small forbs and small perennial grasses. The vicuna is well adapted for such close grazing to the ground by being the only ungulate with open-rooted, continuously growing incisors (Miller, 1924).

VT-3 was common in wet soil types on lower slopes and at the base of slopes. The dominant plant was the stiff-culmed grass Festuca rigesens (Figure 10). Irregularly shaped patches of VT-3 (green in Figure 11) were surrounded by large areas of VT-2 (white in Figure 11) or VT-11 (orange in Figure 11). VT-3 was the prevailing plant community 50 km east of Pampa Galeras in the puna region of Yauriviri where total precipitation was higher than Pampa Galeras. In Yauriviri VT-3 was the result of total accumulative precipitation, whereas in Pampa Galeras this type was a consequence of localized topographical runoff. Production and feeding preference was high and VT-3 received the second highest use of all types of feeding vicunas. VT-14 was the same as VT-3 except Festuca rigesens was the subdominant species in VT-14 (Table 1).

VT-1 was the fifth most common plant community. The dominant perennial grass Calamagrostis vicunarum was a favorite of vicuna. This type had the highest production of all types in 1970 and was preferred by grazing vicuna. Topsoil was the third deepest of all types (Table 1). VT-1 commonly occurred as circular to oblong shaped "putting greens" on the flat where it was surrounded by VT-2 or VT-4 (Figure 12). VT-1 was less densely vegetated on the slopes (Figure 13); these downhill lines had lower production and thicker topsoil than the oblong patches on the bottomland and flat. Vicuna

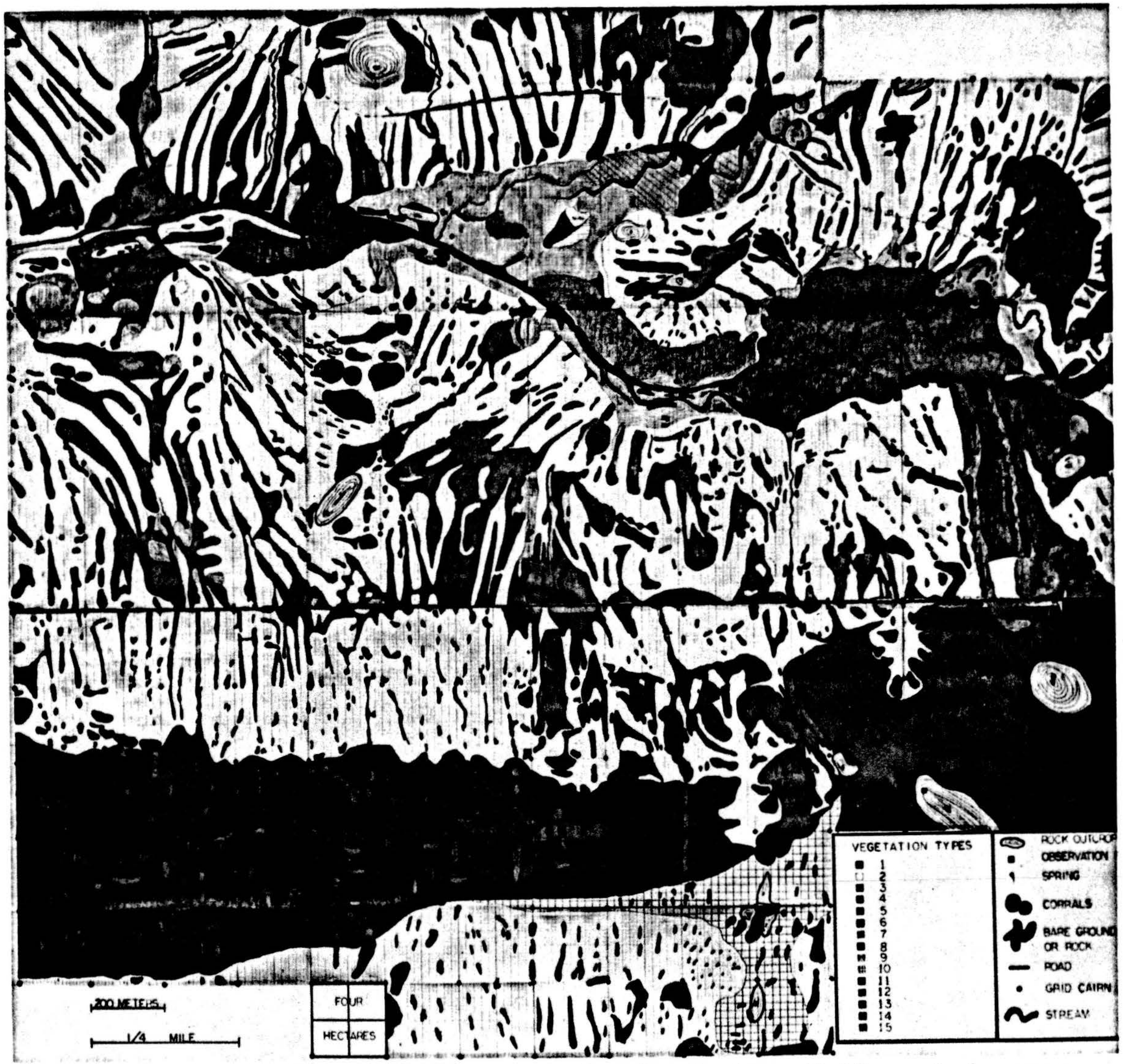

Figure 11. Color photograph of vegetation types in the Cupitay Valley study area.

Figure 12. An oblong patch of the preferred vegetation type-1 dominated by Calamagrostis vicunarum. This type was the terminal seral stage of excrement influenced vegetation.

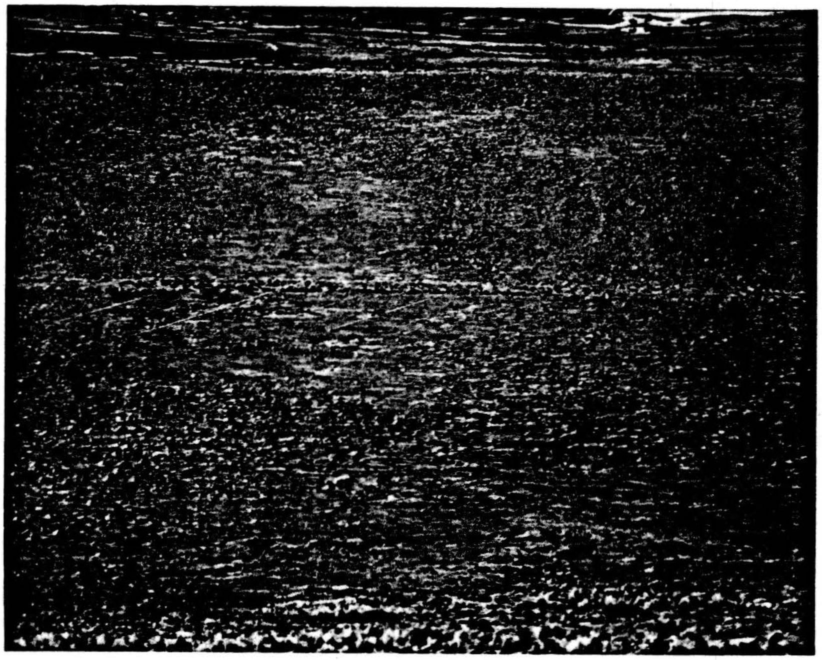

Figure 13. Long linear belt of vegetation type-1 on a slope flanked by vegetation type-2. The small dark circles in vegetation type-1 are vicuna dung piles.

dung piles were found near the top of each oblong patch and along the downhill lines. VT-1 was interpreted as the terminal stage of the vicuna excrement influenced vegetation seres.

VT-6 was a wet and boggy plant community found on the bottomland or around perennial springs on slopes and flats (Figure 14). The dominant plants were coarse in texture and grew close to the ground. Production was intermediate compared to other types; topsoil was the deepest of all vegetation types measured. Vicuna's use of this type was low because of its small area, but preference was high.

VT-7 and VT-15 were composed of nearly the same plant species, but in different proportions (Table 1). They occurred next to each other in the bottomland and took on the appearance of a densely vegetated carpet (Figure 15). Use was low, but vicuna showed a high preference for both types. Alpacas (*Lama pacos*) fed upon these types heavily. Although not measured, topsoil depths were equivalent if not deeper than VT-6.

VT-10 was profusely littered by surface rocks and occurred on the flattened summit of ridges (see background in Figure 16). Topsoil depth was the shallowest of all types, and productivity, feeding use and preference compared to other types was low.

VT-8 occurred on the bottomland and resembled a less densely vegetated form of VT-1 because of the presence of *Calamgrostis vicunarum*. This community was not a type of excrement influenced vegetation, but was primarily related to areas of lowland sediment accumulation. Total use by feeding vicuna was low, but preference was high. Alpacas and llamas (*Lama glama*) grazed heavily upon VT-8.

Figure 14. The marshy vegetation type - 6, dominated by hard cushion plants.

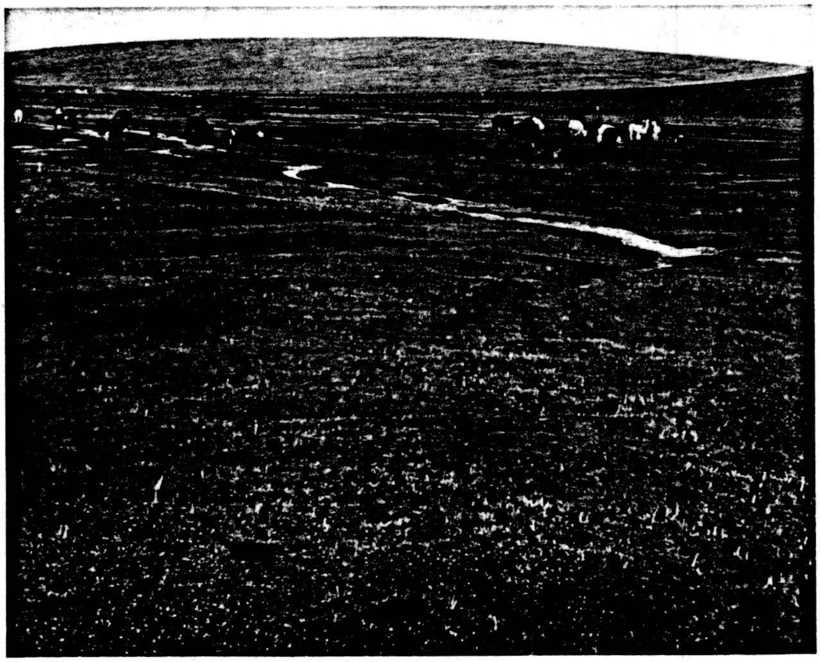

Figure 15. Vegetation type-7, found on the bottomland. Grazing alpaca pictured in the background.

Figure 16. Circular ring of Stipa ichu around a dung pile, the first successional stage of excrement influenced vegetation.

VTs-14, 8, 3 and 1 had the highest plant species diversity and were all preferred by vicuna (Table 1 and Figure 8).

Topsoil depth and plant productivity

The mean combined depth of topsoil horizons A_1 and A_2 for all vegetation types was 20.2 cm and ranged from 11.5 to 25.3 (Table 1). The wetter vegetation types (VT-6) had the deepest topsoils and the driest (VT-10) had the thinnest.

Plant production was estimated during two contrasting years; the growing season was 17 weeks long in 1970 and 8 weeks in 1971. Production averaged 786 kg/ha in 1970 and 474 kg/ha in 1971. Those vegetation types with relatively deep and wet topsoils had the greatest decrease in production (63 percent decrease for VTs 1, 3 and 14). Communities with relatively thin and dry topsoils were least affected by the 1971 short growing season (30 percent decrease for VTs 2, 4, 10 and 11), probably because the xeric plant species comprising those types had shorter life cycles than plant species associated with the wetter vegetation types. Topsoil depth was not related to primary production.

Excrement influenced vegetation

A striking feature of the landscape in Pampa Galeras was the alternating zones of vegetation on the valley slopes. Wide and sparsely vegetated strips dominated by surface rocks alternated with narrow downhill lines of densely vegetated strips dominated by VT-4 or VT-1. Numerous vicuna dung piles were scattered throughout the densely vegetated lines, especially near the top.

Vicuna defecated and urinated only on established and traditionally used dung piles. The long-term deposition and redistribution of nutrients and organic matter at specific spots has caused an acceleration in soil development and plant succession (Franklin, 1973c). The downhill washing of organic matter and nutrients by precipitation and the consequent changes in soil and plant succession, have caused these narrow densely vegetated belts. Such excrement influenced vegetation occurred also on the flats (Figure 12), but there the subsequent change in vegetation around the dung piles was more oblong than linear. Excrement influenced vegetation made up 18 percent of the total surface area in the study area.

During fall, winter and early spring, there was little precipitation; but with the sudden and voluminous summer rains, accumulated excrement and nutrients were washed downhill. It was then that the direct fertilizing effects of excrement and urine could be seen downhill from the dung piles as darker-green plant growth.

Excrement influenced vegetation was also observed in other regions of the puna in southern Peru, where there have been vicuna during the past decade. Inland from Pampa Galeras, the frequency of excrement influenced vegetation with its striking contrast to the surrounding vegetation decreased. Precipitation and soil fertility progressively increased eastward from Pampa Galeras, presumably moderating the fertilizing effects of dung piles. Excrement influenced vegetation is also common around the dung piles of guanaco (Lama guanicoe), the other South American wild camelid (Franklin, 1975a), as well as around corrals of the closely related but domesticated llama and alpaca.

In Pampa Galeras there were three successional stages of vegetation resulting from the vicuna's dung piling behavior: (1) VT-4, which was common as linear downhill lines throughout the Pampa Galeras region (Figure 10), irregularly shaped patches on the flats and occasionally as circular rings around dung piles on level ground (Figure 16); (2) a transitional phase between seral stages one and three; and (3) the terminal stage VT-1. Topsoil depth increased 2 cm with each succeeding stage.

The soil in Pampa Galeras was poor in nitrogen and organic matter. The centralization of these deficient commodities by dung piling behavior resulted in greater soil depth, higher plant species diversity and increased forage production in excrement influenced vegetation.

Effective vicuna habitat in Pampa Galeras Reserve

Forty-three percent of the Pampa Galeras Reserve was unusable or poor vicuna habitat. Unusable bare ground and rock outcroppings accounted for 4 percent of the Reserve. Poor habitats consisted of

VT-4, VT-11 and Tola, a shrub community not found in the study area (Figure 17). Solid stands of VT-4 covered 6 percent and VT-11 26 percent of the Reserve. The Tola community was dominated by Lepidophyllum tola (= Parastrephis lepidophylla) and lesser amounts of Diplostephium spp. Comparison of aerial photos with field conditions revealed that Tola had invaded widely over the past 25 years into the lower end of Cupitay, Huisccana and Llamaiso Valleys where domestic animals, espcially cattle, have heavily overgrazed the previously dominant VT-11. The Tola community accounted for 8 percent of the Reserve.

The downhill lines of VT-4, separated by wide areas of VT-2, together covered 24 percent of the Reserve and were classified as fair vicuna habitat. The remainder of the Reserve (33 percent) included VTs 1, 2, 3, 6, 12 and 13 and was considered good vicuna habitat. Areas classified as fair and good habitat made up 57 percent of the Reserve.

VTs 1, 3, 6 and 8 were key communities with high feeding use and high preference by vicuna. Quality of habitat depended, however, not only upon good forage, but also upon the accessibility of permanent drinking water and a communal sleeping ground (Franklin, 1973c). Unlike the Asian-African members of the camel family, vicuna regularly drink, especially in the dry season when water is required daily. Streams or springs within or on the border of a territory often provided the vicuna group immediate access to water.

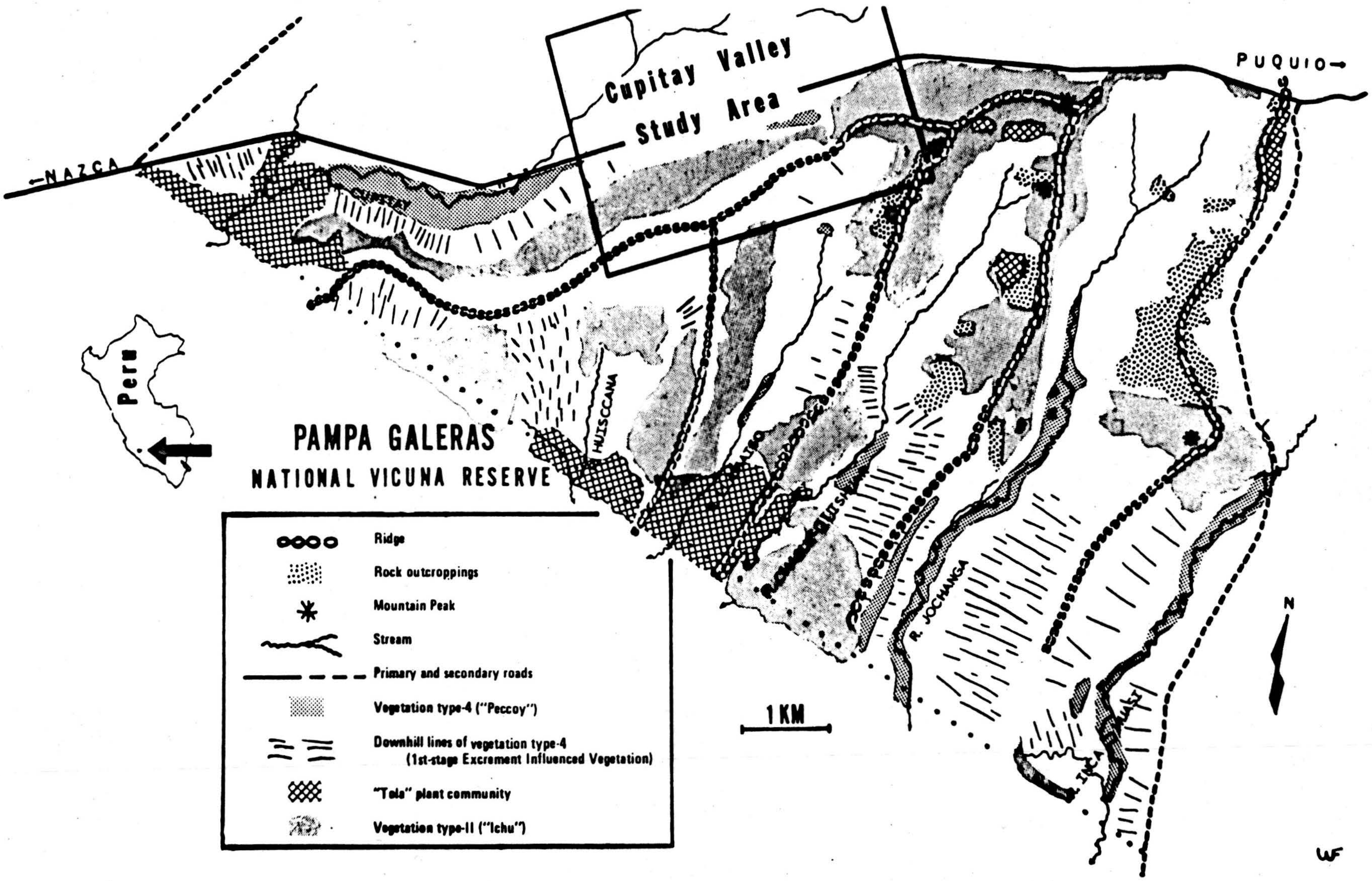

Figure 17. Major plant communities and geographical regions of the Pampa Galeras National Vicuna Reserve, Peru.

Table 2. Vicuna and family group density in usable habitat within the Pampa Galeras Reserve during the 1968 and 1971 censuses.

Drainage	Total area (ha)	Percentage of fair to good habitat	Vicuna/100 ha		Family Gps/100 ha	
			1968	1971	1968	1971
Cupitay	1,200	43	23	39	2.1	6.0
Huisccana	910	52	15	16	1.5	3.6
Llamaiso	776	51	20	63	3.3	9.9
Ch.-Quishuar	1,077	43	26	23	2.8	3.9
Jochanga	1,674	72	25	30	2.8	3.5
Inca Huasi	850	75	30	33	3.8	7.2
Total Reserve	6,487	57	24	33	2.7	5.2

In 1971 Llamaiso Valley had 10 family groups/km^2 of usable habitat and Jochanga Valley had only 3.5 (Table 2). The high density of vicuna in Llamaiso Valley was due to the presence of good vegetation types and closeness to permanent water and sleeping areas. In comparison to Llamaiso Valley, Jochanga was a wide, flat valley with less surface water and greater distances to sleeping grounds. Another factor possibly responsible for the low density of vicuna in Jochanga was the abundance of rock outcroppings, the favored denning habitat of the Andean fox (*Dusicyon culpaeus*), a predator on vicuna.

Population Characteristics

Five vicuna social units were distinguished: Permanent Territorial Family Groups (PTFGs), Marginal Territorial Family Groups (MTFGs), Mobile Family Groups (MFGs), Male Groups (MGs) and Solo Males (SMs). Permanent and Marginal Territorial Family Groups were the most common social units and were composed of one adult male and females with and without crias. PTFGs and MTFGs each occupied a feeding territory where the group spent most of the day and a sleeping territory located on higher terrain where they passed the night. MTFGs were primarily groups from outside of the study area making brief forays into it to drink and graze. Non-territorial males formed all-Male Groups.

Reproduction

Mating season. Breeding was almost an unnoticeable event, except for a short and brief chase before mating and for the fact that the mating pair lay down during a prolonged copulation. An adult female showed no unusual behavior to indicate she was in estrus and the male did not persistently smell the female's hindquarters as is true of so many ungulates. Prolonged preoccupation or tending that ungulate males traditionally show for females in heat was absent.

An exception to this low profile breeding behavior occurred when a yearling female in heat was without established membership in a group. In such cases, her running from one family group to the next resulted in some chasing and confusion when she was being pursued by territorial and non-territorial males.

Twenty-one matings were observed between 28 February and 29 May. April was the peak month for mating (rate = 3.0 matings/100 hours of observation, n = 11), followed by May (1.8, n = 4) and March (1.3, n = 5). Almost all matings were in the morning hours and occurred within the family group's feeding territory.

On three occasions an adult female was seen attempting to mount another female. In one case she succeeded and caused the recipient to lie down, where the two remained for 15 minutes in the normal reclining copulation posture. In a second case 10 minutes before she gave birth, a female in labor attempted to mount another female.

Minimum breeding age, fertility and breeding season. Most females were bred for the first time as 2-year olds, while some mated when 12 to 14 months old. Cardozo (1954) reported gestation as 11 months ± 2 to 3 weeks. Thus most females gave birth to their first cria when 3 years old. Vicunas always give birth to a single offspring.

One-fourth of the 2-year old females were visually assessed as pregnant in early March of 1970 and 1971 (n = 16). A female born and tagged in 1969 gave birth to her first cria in April 1971 when she was 2 years old. During the breeding season estrus yearling females not yet established in a family group might run from one family group to the next and be bred by the resident territorial male in each of several groups.

Females within a few weeks of parturition were visibly pregnant. A high percentage of females 2 or more years old were pregnant: 1969 - 85 percent (n = 162), 1970 - 95 percent (n = 38), 1971 - 85 percent (n = 113). Nonpregnant adults were largely 2-year olds. A lower percentage (10 to 20 percent) of females in MTFGs were pregnant than females in PTFGs.

Ninety percent of the births occurred between 22 February and 7 April (n = 190); three-fourths of all births were in March. The earliest observed birth was on 20 January and the latest on 31 July. Of the 24 births witnessed, 23 occurred in the morning and within a group's feeding territory. Morning births are likely a behavioral adaptation to the Andean stormy afternoons. In summer, daily storms regularly started around noon. Crias born during afternoon storms are not able to dry their soft insulating wool before entering the near freezing nights and would have little chance for survival.

Parturition. My observations on vicuna parturition closely coincided with those of Koford (1957). A female about to give birth separated herself 15 to 25 m from the group. During the usual 1-hour labor the female often looked back to inspect her hindquarters, lay down and stood intermittently, changed positions and walked several steps every few minutes. Birth occurred while the female stood. She immediately smelled and inspected the head and muzzle of the newborn, but no licking occurred nor was the placenta eaten. Other group members frequently came over to smell and inspect the newborn shortly after birth. Fifteen to 20 minutes after the birth, the cria was on its feet. It began nursing when 30 to 45 minutes old.

Females seemed to delay parturition until they arrived at their feeding territory. A group displaced from its territory by domestic animals or people and containing a female showing early signs of labor (raising tail frequently, restless and walking about near group), soon returned to its feeding territory where the female gave birth. For example, on the morning of 2 March 1971, MTFG 209 was 2 hours late in reaching its feeding territory. Within an hour after arriving, a female gave birth to a cria.

On one occasion a group with a female about to give birth was approached in hope of tagging the newborn cria, but the group ran off. The cria was half protruding from the female as she ran with the group for 1.5 km before she stopped and gave birth. She quickly inspected it and continued her flight without the cria. Five hours later the tagged cria was carried to the group's sleeping territory and left. The next morning the cria was with its mother despite the initial separation. Three other cases occurred when the cria was temporarily separated from its mother within minutes after birth, handled by people for tagging and left in the group's territory. Each time it was fully accepted and reunited with the female. These experiences suggested female vicuna rapidly imprint upon their newborn young.

Vicuna crias are followers as opposed to hiders (Lent, 1974); from birth crias stay close to their mothers during daily movements. During the first few days after birth mothers were unusually leery and flighty. Such females sometimes arrived at the feeding territory with their crias an hour or two after the group. Females with very young crias sometimes attempted to leave the feeding territory and return to higher ground in the direction of their sleeping territory during midday, although the male usually prevented them from doing so. Disturbance by humans, domestic stock and dogs on the slopes and valley floor was the suspected cause of the female's uneasiness. Crias were weaned in July and August when 4 to 6 months old, but occasionally attempted to nurse as late as November.

<u>Reproductive success.</u> Four months after the beginning of the birth season the maximum ratio of crias to females was reached (Figure 18). In June 1969, 74 percent of the females had crias at

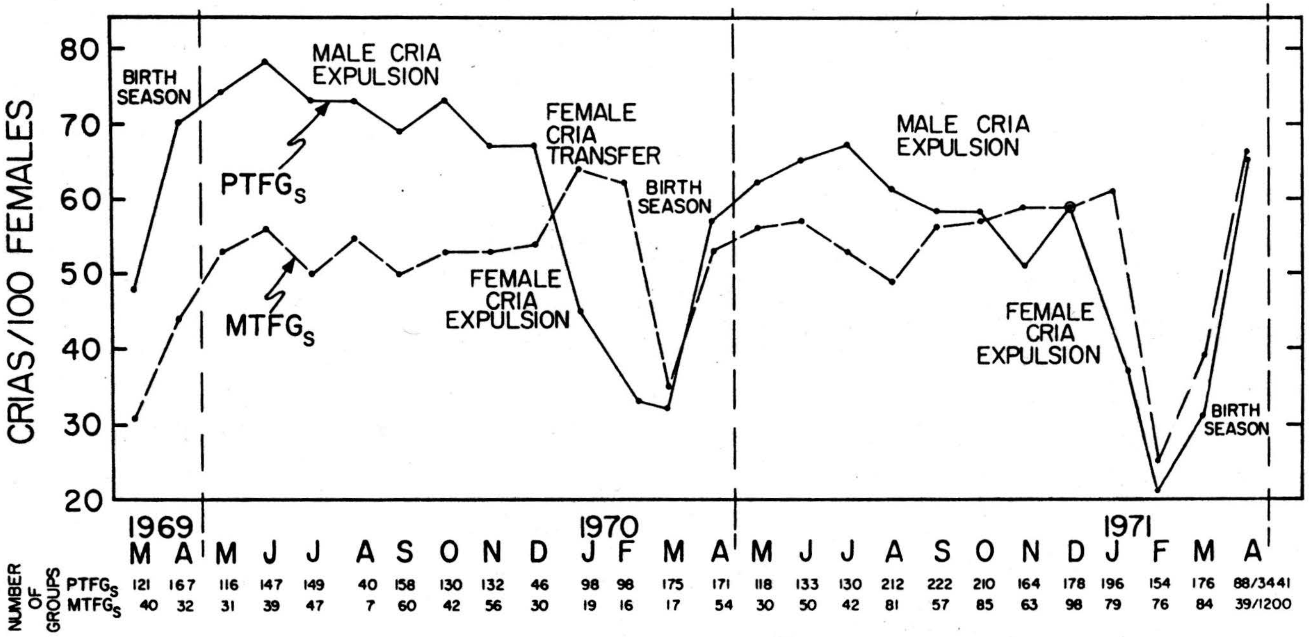

Figure 18. The number of crias per 100 females (2 years and older) for PTFGs and MTFGs in observation Zones I and II combined.

their sides (n = 740 females, 186 family groups); in June 1970, only 63 percent had crias (n = 596 females, 183 family groups). Before the birth season, 85 and 95 percent of the females were pregnant, indicating that some 10 percent (1969) to 30 percent (1970) of the crias born died during the first 4 months. The cause of the cria mortality was not determined, but predation was suspected. MTFGs had lower reproductive success than PTFGs (Figure 18).

The cria to adult female ratio had the most meaning as a measure of reproductive success and cria survival from July through October. The cria to adult female ratio remained relatively stable during this period although some juvenile males were forced from their family groups by the adult males. The ratio became increasingly less meaningful from October through February when juveniles were being expelled from their groups.

Reproductive success varied between geographical regions within the Pampa Galeras Reserve. In August 1968, cria to adult female ratio was the lowest in Jochanga Valley (35:100), highest in Huisccana Valley (70:100) and averaged 48:100 for the entire 6,500 ha Reserve. Poor habitat and possible fox predation were suspected causes of low cria survival in Jochanga Valley. Reproductive success and cria survival were higher (67:100) in the Cupitay study area than most areas of the Reserve.

Numbers and density

From the early 1950s to mid-1960s the total vicuna population plummeted from 400,000 (Koford, 1957) to possibly as few as 5,000

(Grimwood, 1969). Illegal hunting for the vicuna's soft and high priced wool was the primary factor responsible for this sudden crash.

There was doubt that the vicuna would be able to recover its numbers because of its low reproductive rate. The International Union for the Conservation of Nature (1968, p. MA117) reflected this concern when it reported that "Infant mortality is apparently high . . . ratio of juveniles to mature females at the end of the season of birth was 46 to 100. Gestation . . . about 11 months . . . a single offspring." Fortunately, this early concern proved unfounded at Pampa Galeras, where numbers have substantially increased since establishment of the Reserve in 1966.

Within the Reserve, vicuna increased at an annual rate of 16 percent with a total increase of 50 percent (814 to 1,217) from 1967 to 1971 (Franklin, 1973c). In the 1972 census (complete count) conducted by the Reserve's game guards, 2,095 animals were counted within the Reserve (Norberto Mayorga, personal communication), representing nearly 160 percent increase in the 5 years since 1967. The same 1972 census showed 7,291 vicuna in the entire Pampa Galeras region. The 1975 census, covering 60,000 ha in and around Pampa Galeras, showed 12,816 animals (Carlos Ponce, personal communication).

Stricter laws against hunting (Franklin, 1969) and improved law enforcement have been highly successful in reversing the vicuna's decline. The contribution of Pampa Galeras, where as much

As the population increased, the density of PTFG animals in Zone II decreased from 16 to 11, while MTFGs increased from 3 to 4 and MGs increased from 4 to 7 vicuna/km^2 (Figure 19). Total animal density decreased 8 percent in Zone II during the study. On better vicuna habitat (Zone I) the density of PTFG animals increased from 15 to 17, MTFGs increased from 1 to 2 and MGs increased from 2 to 3 vicuna/km^2 (Figure 20). Total density in Zone I increased 22 percent. Thus, an area of good habitat had a small increase in animal density, while secondary habitat had a marked decrease of PTFG animals and an increase in use by visiting MTFGs and MGs. Overall, the density of PTFGs was four to six times more than that of MGs and MTFGs.

Seasonal changes of vicuna density in good habitat were regular and predictable due to a relatively stable adult female population, regular seasonal increase from births and subsequent decrease from cria dispersal (Figure 20). In secondary habitat the density of animals in all social groups, especially MGs and MTFGs, was much more irregular and fluctuating (Figure 19). At the end of each dry season in Zone I the density of MGs and outside MTFGs increased when these groups left their waterless habitat for daily drinking visits to Zone I (Figure 19). The same increase of MTFG density occurred in Zone II during the late dry season. The mean maximum number of PTFGs observed per hour increased 33 percent (9.2 to 12.2) within the study area from Year One to Year Two, while MTFGs increased 68 percent (1.9 to 3.2) and MGs increased 43 percent (0.7 to 1.0).

as three-quarters of the world's surviving vicuna are found, has been paramount (Franklin, 1975b).

In 1968 there were 14 vicuna/km^2 within the Pampa Galeras Reserve. Three years later in 1971 density increased to 19 vicuna/km^2. The density of vicuna on fair to good habitat (effective) increased from 24 to 33 vicuna/km^2 between the August 1968 and December 1971 censuses. Effective habitat per family group decreased 48 percent as the number of family groups increased from 2.7 to 5.2/km^2. The 2,095 vicuna counted within the Reserve during the 1972 census placed the gross density at 39 vicuna/km^2, a level considered by Koford (1957) near the carrying capacity of vicuna range. The density of animals in the 1975 census was 21 vicuna/km^2. In the area studied by Koford (1957) between Puno and Arequipa 400 km southeast of Pampa Galeras the density was 39 vicuna/km^2.

In the Cupitay Valley study area from Year One to Year Two density rose from 19 to 22 vicuna/km^2. Zone II was poor habitat compared to Zone I because water and key vegetation types were much less abundant. Contrary to what one might expect, the poorer habitat had higher mean density over two years than the better habitat (23 vs. 20 vicuna/km^2). The reason for this was that the PTFGs dominated the best habitat. MTFGs and the large MGs were forced into the poorer habitat of Zone II. This was presumably possible because the nonbreeding males of MGs had lower nutritive requirements than did breeding females and because of the highly aggressive males of PTFGs.

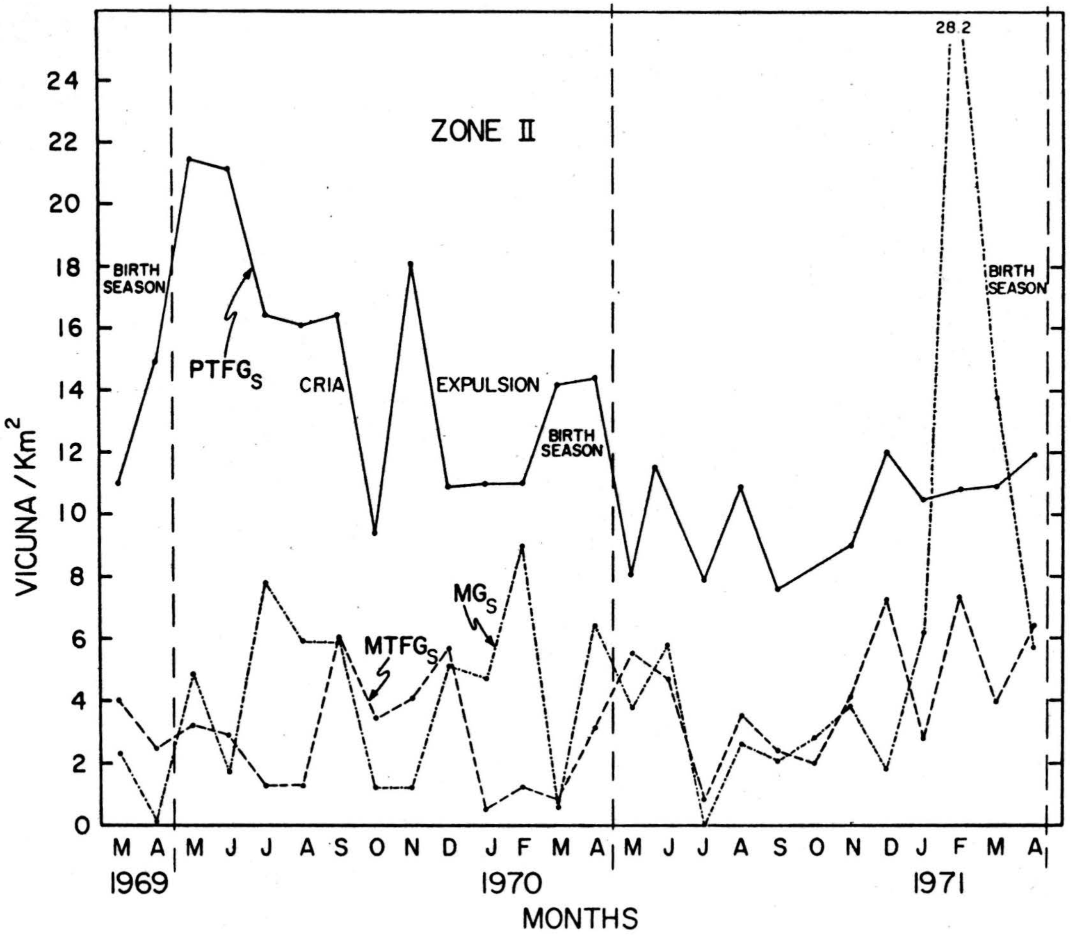

Figure 19. Monthly density of vicuna social groups in an area of secondary habitat.

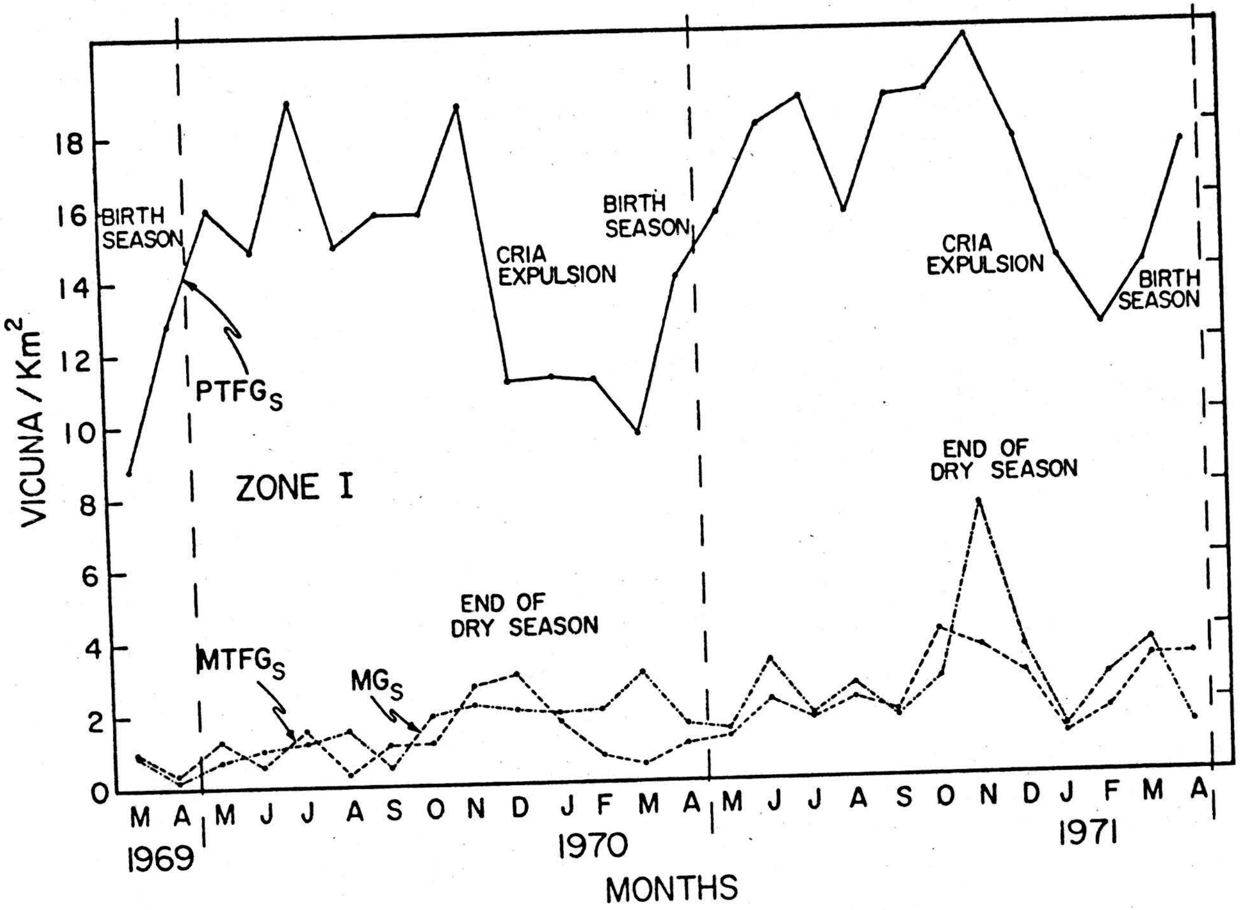

Figure 20. Monthly density of vicuna social groups in an area of good habitat.

Size and composition of vicuna social groups

Vicuna family groups averaged 6 and MGs 22 animals (Table 3). Fifty-one percent of PTFGs had from one to five animals, 38 percent six to ten and only 11 percent with over 10 animals. Three-quarters of all MGs had fewer than 30 animals and 5 to 10 was the most common group size. Male groups with greater than 50 animals were more prevalent in spring and summer when yearling males joined them. Zone II had a higher percentage of large male groups than did Zone I.

The largest family group observed during the study had 19 animals (PTFG 207 with one adult male, 10 adult females and 8 crias in June 1969). The largest male group seen had 155 animals.

The composition of family groups was written as an abbreviated formula: total number of animals in group (adult male - adult females - yearlings - crias), e.g. 19(1-10-0-8). The average composition of PTFGs was 6.1 (1.0 - 3.2 - 0.1 - 1.8) and of MTFGs 5.1 (1.0 - 2.6 - 0.1 - 1.4).

Changes in size and composition of PTFGs and MTFGs

The size and composition of PTFGs and MTFGs were highly influenced by births and dispersal of young. During the summer birth season the number of crias increased (Figures 18 and 21). Over the next 6 months, the ratio of crias to adult females declined moderately in PTFGs as adult males drove out male crias and some mortality of crias occurred. MTFGs maintained themselves

Table 3. Mean size of vicuna social groups and change over two years.

Social Group	Year One (May 1969-April 1970)	Year Two (May 1970-April 1971)	Percent Change
PTFGs	7.0	5.4	-23%
S.D. =	(3.8)	(2.3)	
N =	(1,460)	(1,981)	
MTFGs	5.3	5.0	- 6%
S.D. =	(2.6)	(2.3)	
N =	(417)	(783)	
MGs	21.9	22.1	+ 1%
S.D. =	(16.3)	(17.8)	
N =	(143)	(246)	

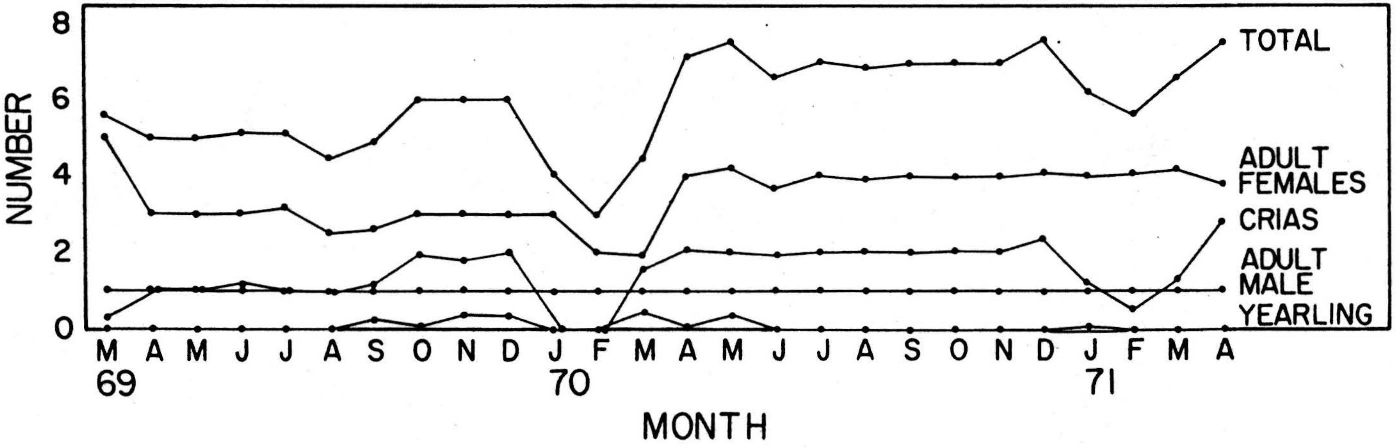

Figure 21. Number of animals in PTFG 216.

at about the same size because some male crias driven from PTFGs entered MTFGs. In December and January female crias and any remaining male crias were expelled from PTFGs, with many of the female crias joining MTFGs. In February, just before the next birth season, these crias were also forced from the MTFGs; and both MTFGs and PTFGs reached their lowest ratio of crias to adult females in March.

In most PTFGs all crias were forced out before the next birth season. However, due to averaging data by months and because some female crias transferred to groups in which the male was forming his family group, the cria to adult female ratio did not drop below 32:100 in Figure 18. PTFG 216 clearly showed this period when crias were completely absent from most PTFGs (Figure 21).

Changes in size and composition of MGs

Continuous day-to-day information for particular Male Groups was impossible to obtain because the groups constantly changed in number and location. Koford (1957) also reported far-ranging movements by MGs. An example of how MGs changed in size was observed on 11 September 1969: at 0800 a MG had 15 animals; at 0900, 25 animals; and at 1200, 36 animals. Such splitting, mixing and joining of MGs was common.

When juvenile males were expelled from their groups, they joined MGs. Male crias were especially common in MGs in January and February; for example 7 male crias in a MG of 15, 32 male crias in a MG of 61 and 6 male crias in a MG of 49. Male crias were usually part of a mixed MG of juveniles and adults; but small juvenile groups of two to five animals also occurred, particularly in February. Within a few weeks, juvenile male groups also joined MGs containing older age classes.

Relative proportion of social groups

Over 2 years, 59 percent of all animals were in PTFGs, 17 percent in MTFGs and 24 percent in MGs. Three out of every four family groups were PTFGs and about one third of all males older than 1 year held territories (Table 4).

From 1968 to 1971 the portion of the population in family groups in the total Reserve increased from 76 percent to 81 percent, and the number of family groups increased from 101 to 193 (Table 5). The ratio of females to males in the 1971 census was 100:85. Nine out of every 10 groups identified were family groups. As the population increased from 1968 to 1971, vicuna pushed out into vacant and often less desirable range. The number of adults per family group decreased from 4.9 to 3.7, partly because newly formed family groups tended to be smaller than established ones, but perhaps also because the amount of effective habitat per group decreased.

During a 3-day field trip in 1968 to Yauriviri, southeast of Pampa Galeras, only five vicuna family groups were seen. Although a small sample, the mean group size of 9.4 at the low vicuna density in Yauriviri was the converse of the mean group size of 4.9 at high density in Pampa Galeras.

Table 4. Percentage of animals seen in vicuna social groups.

Social Group	Percentage Year One (May 1969-April 1970)	 Year Two (May 1970-April 1971)	 Change
PTFGs	66	53	-13
MTFGs	14	20	+ 6
Male Groups	20	27	+ 7
Total	100	100	-
N =	15,554	19,995	-
Percentage Of All Adult Males Territorial	32	27	- 5

Table 5. Changes in vicuna population size and structure between August 1968 and December 1971 in the 6,500 ha Pampa Galeras Vicuna Reserve.

Population Character	1968	1971	Percentage Change
Total population	891	1,217	+ 37
Number of family groups	101	193	+ 91
Mean family group size	6.7	4.9	- 27
Mean number of adults per family group (> 1-year old)	4.9	3.7	- 25
Number of male groups	11	27	+146
Mean male group size	19.2	17.2	- 9
Percentage of groups that were family groups	90	92	+ 2
Percentage of population in family groups	76	81	+ 5
Percentage of all males territorial	32	45	+ 13
Percentage of population as solo males	0.2	1.1	+0.9

Dispersal of yearlings

When male and female crias approached one year of age and were forced from their family groups, most dispersed from the study area. The number of 8-month old female crias seen per hour during the first week of December 1969 was 4.3. Twenty-five weeks later, when they were about 14 months old, only 0.3 were seen per hour. The 1970 female cria cohort decreased similarly from 8.0 to 2.1. The yearlings that did remain attached themselves with territorial males. Thus, in mid-April 1971 of the 20 yearling females remaining in the study area, 35 percent were with males that had recently established their territories, 27 percent were with long established PTFGs and 35 percent in MTFGs.

By June only 13 percent of the territorial groups (n = 47) using the study area had yearling females: two groups out of 23 PTFGs took on five yearlings (two in one group and three in the other); two groups out of 17 MTFGs took on five yearlings (one in one group and four in the other); and two recently established territorial males out of seven took on six yearlings (three in each group). Very few territorial males were willing to take on more females. This was supported by observations of yearling females being chased by territorial males away from one family group to the next as yearling sought entry into a group. Thus, most yearling females dispersed from an area of good habitat occupied by PTFGs. The few that stayed primarily joined other groups that contained other yearling females.

Mortality and suspected predation

It was uncommon to find dead vicuna in Pampa Galeras. From July 1968 to March 1971, 35 dead vicuna were found by the Reserve's guards while on patrol over the Pampa Galeras region and by myself from within the Cupitay Valley study area: 19 were probably killed by predators, nine by lightning, one by a fall, one from giving birth and five from unknown causes.

The Andean fox, domestic dog (*Canis domesticus*) and puma (*Felis concolor*) are believed to prey on vicuna. Eight dead vicuna with severe throat bite wounds were considered to be predator kills. Fresh fox tracks were found around three of the carcasses. Foxes may even take healthy adult vicunas. An adult female suspected to have been a fox kill was fat and in good physical condition. Of the eight predator kills, there were four adult females, one adult male, and two crias and an adult of unknown sex. Six of the eight were found in or within a few meters of a stream bed. Excluding the mortalities caused by lightning, accidents, or birth, 17 of 24 dead vicuna were found within 10 m of a stream.

Vicuna found within a few meters of a stream were suspected predator kills, since foxes were known to use streambeds and gullies for attacking their prey. For example, on 19 November 1969 at 1130, a single fox was seen to attack from its stream bed hiding place a sheep that was feeding immediately next to the stream. The sheep was pulled into the gully by the fox, but escaped when the sheepherder and her dogs came running and chased the fox away. The North American coyote (*Canis latrans*) will also use gullies and the rough terrain of river bottoms for attacking prey (Davenport, et al., 1973). Of the 17 vicuna found near streams where sex or age was known there were 14 adults, one yearling, no crias and two of unknown age; eight were females, four males and five of unknown sex. Crias killed by predators may have not been found, since the large Andean fox could have readily dragged small crias away to their fox dens.

Vicuna often mobbed domestic dogs and foxes. Simultaneously, several vicuna would vigorously chase and attack the potential predator. Vicuna were especially prone to chase dogs and foxes in the vicuna birth season.

Lightning storms were common during summer. Nine vicuna were found killed by lightning during January, February and March. Storms usually caused vicuna to stop grazing and lie down with their backs to the wind and heads and necks flat to the ground, perhaps in protection from both wind and lightning.

Social Organization

A Permanent Territorial Family Groups (PTFGs) averaged six members: one adult male, three females and two crias. Vicunas in PTFGs composed about 60 percent of the total population. Their territory was in two parts: a feeding territory where the group spent most of the day feeding and a sleeping territory located on higher terrain where they spent the night. An undefended neutral corridor connected the feeding and sleeping territories. The group feeding territory and sleeping territory and connecting corridor were considered its home range. The PTFG feeding territory included access to permanent drinking water. Territories were exclusively occupied by the resident family group and defended by the adult male against all intruding outside vicuna. Size and shape of feeding territories changed from one season to the next, but remained in the same basic location for the entire year. PTFGs occupied the preferred habitats that were found on the slopes, flats and bottomlands (Figure 22).

Marginal Territorial Family Groups (MTFGs) averaged one adult male, three adult females and one cria. There were found on secondary habitat surrounding the better areas occupied by the PTFGs. MTFGs were especially common on the flattened ridges and drier slopes without springs (Figure 23). PTFGs and MTFGs were the primary social units of the vicuna population, in that they were the minimal social unit needed for successful reproduction (Brown and Orians, 1970). Family groups were categorized as PTFGs or MTFGs in order to study the differences between groups occupying good and poor habitat. Some family groups were intermediate between the two categories. Vicunas in MTFGs comprised almost 20 percent of the total population. The size, shape and location of their feeding territories changed more than the territories of the PTFGs. The feeding territory commonly did not include permanent water. As a result, MTFGs spent less time in their feeding territory during the dry season than PTFGs because of daily movements to water.

Mobile Family Groups (MFGs) were a temporary association of females with an adult male that did not have an established territory. Besides the male the group included from one to four other animals,

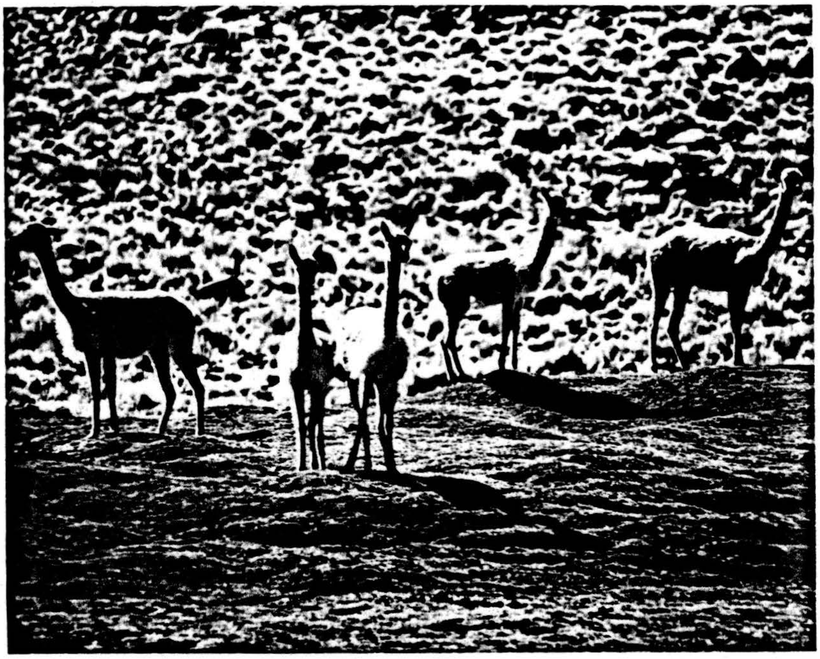

Figure 22. A Permanent Territorial Family Group of vicuna in its feeding territory of good habitat.

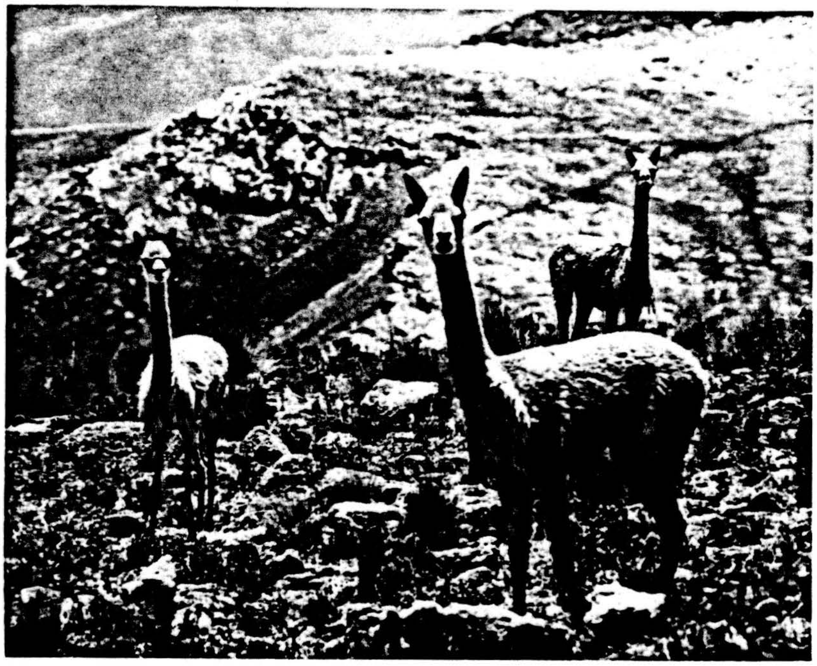

Figure 23. A Marginal Territorial Family Group of vicuna on secondary habitat.

usually one adult female and two or three yearling females (Figure 24). It was difficult to obtain continuous information on any one MFG from day to day because of their high mobility and changing group size. MFGs were seen most commonly during that time of year when crias had been expelled from their family groups. Most MFGs seen in January through March were composed of non-territorial adult males that had secured one or more young yearling females which had been expelled from their family groups. MFGs were chased out of areas occupied by PTFGs and MTFGs, consequently, MFGs spent most of their time on poor habitat.

<u>Male Groups</u> (MGs) were bands of 2-155 non-territorial males (Figure 25). Territorial males vigorously attacked and chased MGs out of occupied habitat. As a result, MGs spent most of their time in unoccupied and non-preferred habitats. MGs moved long distances in search of areas to feed undisturbed. MG size fluctuated often due to subgroups leaving and joining.

<u>Solo Males</u> (SMs) were physically and sexually mature individuals that had left their MGs to establish territories (Figure 26). SMs did much wandering while looking for suitable unoccupied or poorly defended sites to establish their territories. They were aggressive toward established males that attempted to force them from zones with territories. Once a Solo Male had established his territory, it still might take him several months to obtain females.

Figure 24. A Mobile Family Group of vicuna composed of a non-territorial adult male and two young-yearling females.

Figure 25. A Male Group of vicuna whose average size was 22 animals.

Figure 26. A Solo Male vicuna with an established territory but without a family group.

Figure 27. Intergroup Encounter Type III during which a territorial male is chasing the adult female members of a trespassing group from his territory but not making contact with them.

Old or injured males no longer able to hold a territory were occasionally seen by themselves, but were not considered part of this category because of their very small numbers and lack of social involvement with the remainder of the population.

Groups that could not be identified as either a family or male group, wandering adult female-cria pairs and solo yearlings and adult females, were referred to as Unclassified Groups.

Relations Between Social Groups

Aggressive encounter types

Territorial males commonly defended their territories against trespassing vicuna. Eight types of aggressive encounters between groups were recognized. In the first four types the territorial male chased and interacted with a recipient family or male group. Encounter Types 5 and 6 involved no chasing; instead, the initiator male posted himself near his territorial boundary to check the forward movement of a neighboring group into his territory. In Encounter Types 7 and 8 only the two neighboring territorial males interacted with chasing and fighting. Definitions follow:

ENCOUNTER TYPE I occured when the initiator male left his group and trotted or ran toward the recipient group. The recipient group retreated from the initiator male who did not come within 20 m of the recipient group.

ENCOUNTER TYPE II was the same as Type I, except the male came within 20 m of the recipient group, but did not enter the group, nor did he chase or make contact with recipient group members.

ENCOUNTER TYPE III was the same as Types I and II, except the male entered the recipient group, usually chasing one or more adult female members, without making contact. The male of the recipient group would normally attempt to intervene and prevent the attacking male from chasing his group members (Figure 27). Not all pursuits of MG members involved running and chasing. When forcing a MG out of his territory, the defending male would also make short charges toward individual males.

ENCOUNTER TYPE IV was the same as Type III, but the attacking male made contact with a recipient during the chase. When the attacking male chased an adult female in the recipient group, he often attempted to bite at her underside and sometimes tried to knock her down or trip her.

ENCOUNTER TYPE V occurred when the initiator male moved toward the neighboring recipient group at a walk, trot, or run. He did not enter the recipient group, but stopped short to stand, feed, or lie down. He located himself near the recipient group, on or very close to his territory boundary. The recipient group did not flee, but commonly continued to feed without further forward movement. The male of the recipient group did not come forward to confront the initator male. When a male was away on a prolonged Type V encounter his group continued feeding, but often moved in his direction.

ENCOUNTER TYPE VI was the same as Type V, but the recipient male came out of his group to confront the initiator. The recipient usually stood between his group and the initiator male. The two males might approach each other within a few meters and even walk together, but without chasing or contact.

Two neighboring groups that came together at their mutual border while feeding often continued feeding tranquilly in place with each remaining in its respective territory. If one male moved forward between the two groups, the second male did also, thus preventing the other male from charging or chasing his females.

ENCOUNTER TYPE VII was the same as Type VI, but one male chased the other without making contact. Encounter Types VI and VII were especially common between two new territorial neighbors when they were establishing and learning mutual boundaries. They spent long periods within a few meters of each other, separated by their common border and often trotted with their heads immediately next to the ground. The males frequently stopped on dung piles to defecate or exhibited the preliminary behaviors associated with defecation-urination, but didn't eliminate. Such displays were emphasized by prolonged squatting over dung piles for several minutes.

ENCOUNTER TYPE VIII was the same as Type VII, but the fighting males made contact during the chase. Fighting between males occurred year-round with a slight increase in frequency from May to August. Seventy percent was caused by Solo Males attempting to steal females from established family groups, in which case, the resident male defended his females by fighting off the outside male. The balance of fighting was over territorial possession and boundaries between established territorial males.

Fighting usually involved long hard running chases with males attempting to bite and trip each other. Several severe fights lasted the entire day and continued into the next.

Types VI, VII and VIII were helpful to an observer for delineating territorial boundaries, especially Type VII when the two males made short charges back and forth in a seesaw effect at the mutual boundary.

Occurrence and duration of encounters

Of all the territorial defenses observed (n=85,145), 71 percent were Types I, II and III. Only 2 percent were Types IV and VIII. Defending males positioned themselves near the recipient group and their common border (Type V) in 18 percent of all encounters. Encounters where only the two males interacted (VI, VII and VIII) averaged 11 percent over two years. Thus, the most frequent form of territorial defense was by chasing without contact.

The durations of intergroup encounters were recorded for the male of group 211 from April 1970 to January 1971. Territorial defenses ranged from 1 to 57 and averaged 9.6 minutes (n=129) in duration (Table 6). Chases after trespassing groups (Type I) were only 5.4 minutes in duration, but if the encounter involved contact with recipient group members, it lasted nearly three times as long (14.7 minutes) ($P<.05$). The duration of Encounters I through IV

Table 6. Duration of aggressive encounters for male 211 when defending his territory.

Encounter type	n	Duration In Minutes Mean	S.E.
I	56	5.4	1.1
II	10	7.1	2.6
III	11	9.6	2.4
IV	3	14.7	4.8
V	26	11.7	1.6
VI	20	20.2	1.9
VII	3	4.0	4.8
VIII	0	--	--
Combined	129	9.6	0.5

increased progressively. A confrontation of both males at their mutual border without chasing (Type VI) was the longest lasting encounter ($P<0.05$), but when they chased each other (Type VII) the encounter was five times briefer.

Resident PTFG males chased MTFGs (148 m) and MGs (140 m) further than they did neighboring PTFGs (117 m) in Encounter Types I through IV ($P<0.05$; n = 800). Encounter Types V and VI without chasing were significantly ($P<0.05$; n = 350) shorter (54 m) than those with chasing (130 m), while chases between territorial males

(Types VII and VIII) averaged the same distance (130 m) as territorial males chasing trespassing groups (Types I to IV). There was a sharp increase in the total mean distance fighting and chasing males covered from the first (91 m) to the second year (160 m).

Daily and seasonal changes in types of encounters

Males defended their territories throughout the day, but especially in the morning (75 percent, n = 8,177) (Figure 28). As the density of groups increased 45 percent over two years, the frequency of encounters also increased (Figure 29). Peaks in the rate of encounters coincided with the breeding season, or when MG or MTFG density was up. The low intergroup encounter rate in September 1970 corresponded with a decrease in animal density. In both years, males protected their territories more during the birth and breeding periods.

Encounter Type I was the most common during Year One and Type II in Year Two (Figure 30). In the second year, when group density was up, defending males significantly ($P<0.05$) approached the recipient group more closely and entered it more often (Types II and III). Thus, the vigor or intensity of territorial defense increased as group density increased.

Encounters between social groups

Nearly half of all encounters by a PTFG were with a neighboring PTFG, 35 percent with MTFGs visiting the study area, and 16 percent with MGs (Figure 31). The proportion of encounters with MGs and

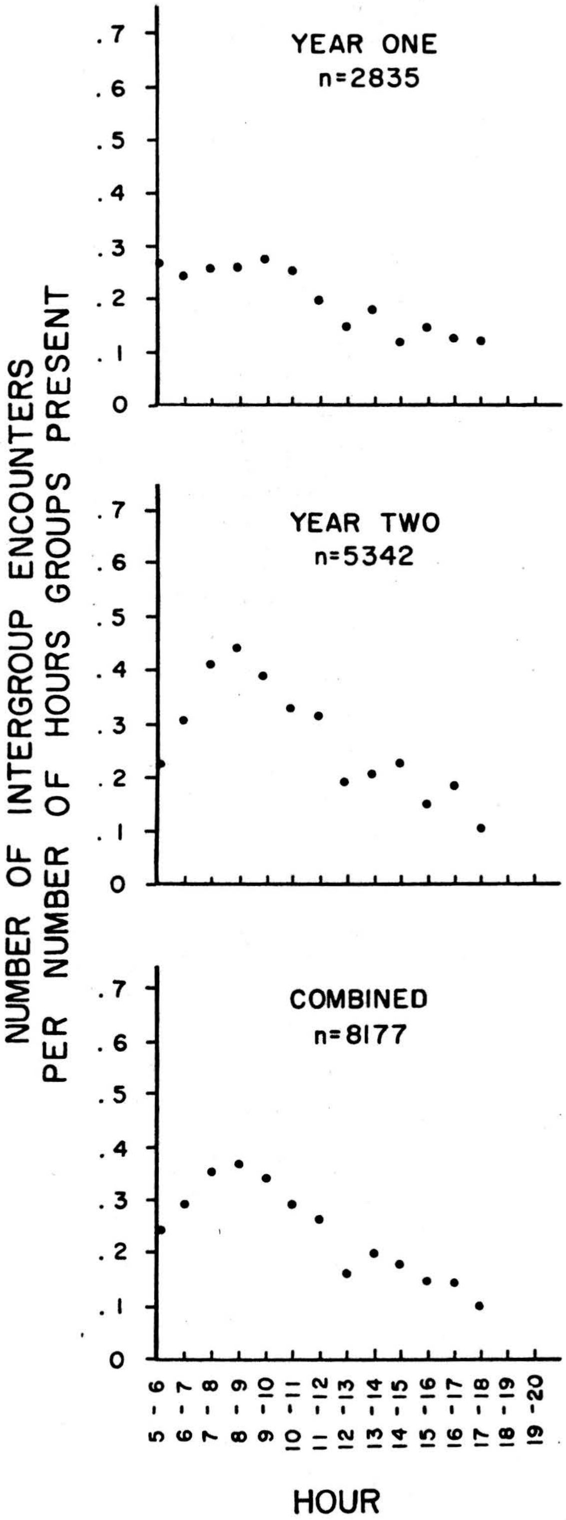

Figure 28. Rate of territorial defense compared to the time of day.

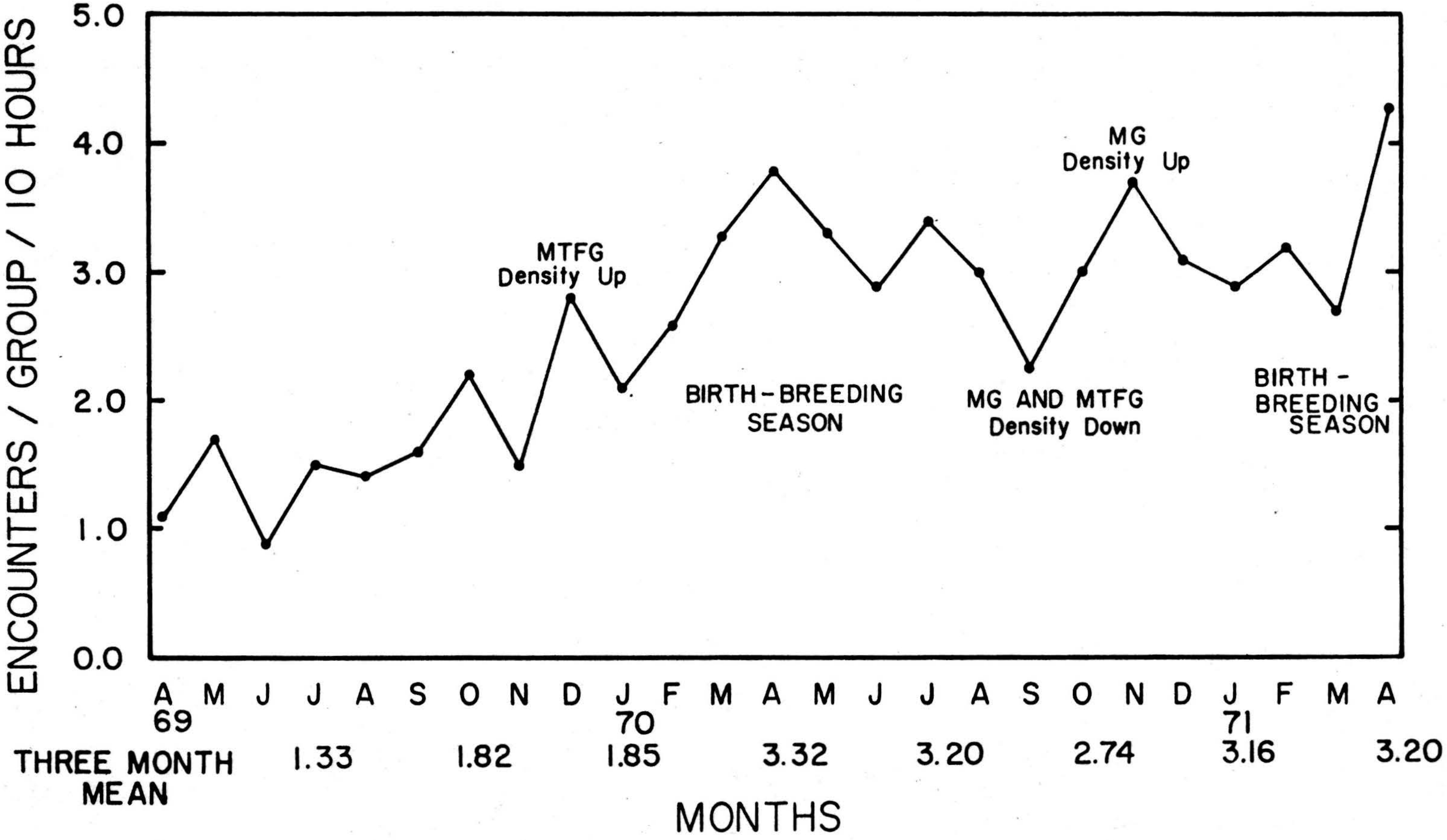

Figure 29. Rate of territorial defense related to the time of year and three month means of rate beginning in May 1969.

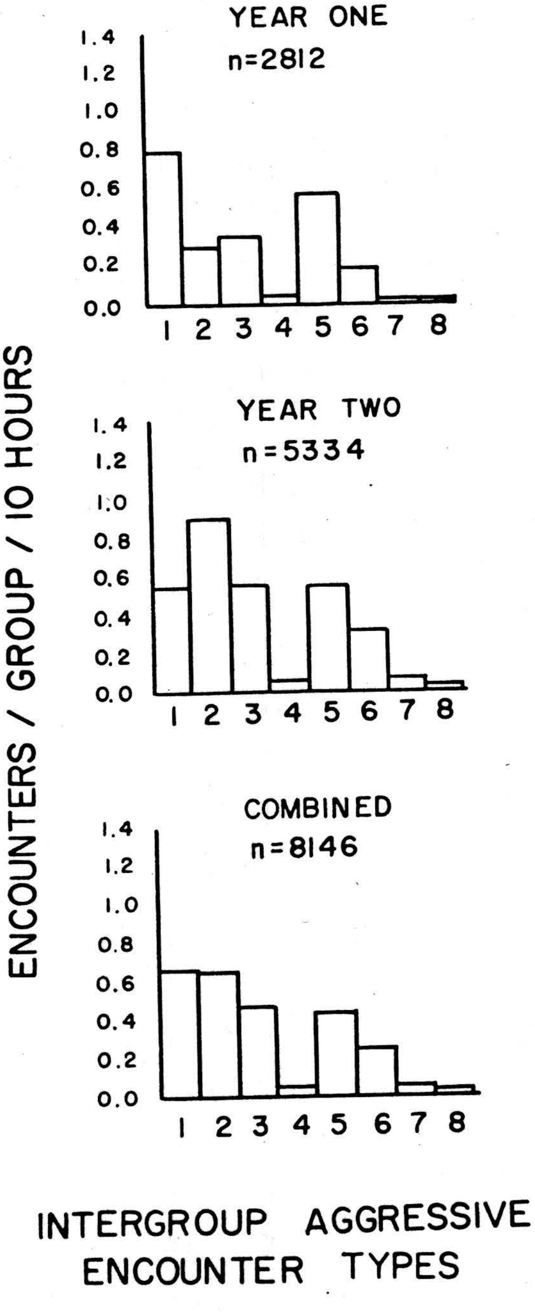

Figure 30. Changes in the rate of territorial defense types over two years.

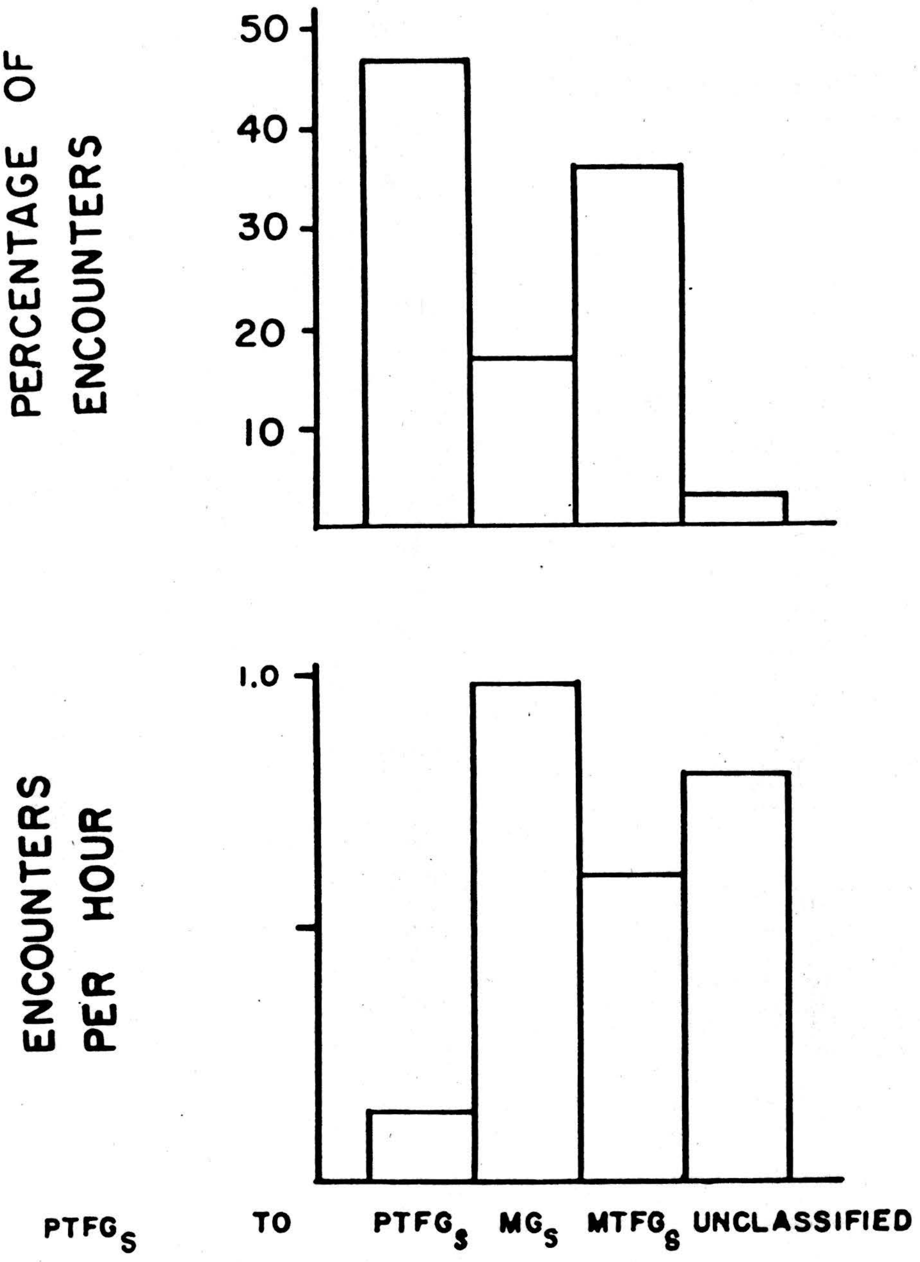

Figure 31. The proportion and rate of territorial defense encounters from Permanent Territorial Family Group males to other social groups (n = 7,097). Rate based upon the number of hours recipient group was present.

unclassified groups was constant from the first year to the second. However, there was a 6 percent decrease in the proportion of encounters between PTFGs and a 7 percent increase between PTFGs and MTFGs as the latter increased in density by one and a half times ($P<0.05$).

Rates of aggression towards different types of social groups were obtained by counting the number of encounters per hour per group present (Figure 31). The probability of PTFGs interacting with each other rather than with MTFGs and MGs was much higher, since there were three times as many PTFGs as MTFGs and MGs combined. Territorial males showed the highest level of aggression towards male groups (1.0 encounters/hour) and the least towards neighboring PTFGs (0.1 encounters/hour). Aggression was also high towards MTFGs and unclassified groups. Thus, territorial males were much more aggressive towards MGs and to family groups from outside the area than to locally established family groups. The rate of aggression towards the local PTFGs remained constant over 2 years, while the rate towards MGs increased 25 percent, MTFGs 30 percent and unclassified groups 64 percent ($P<0.05$), even though the density of all social group types increased. Peaks of aggression towards Male Groups were during the summer of Year One when MGs were harrassing family groups and in spring of Year Two when MGs were seeking sources of water. An example from mid-November, 1970, illustrates the high rate of aggression MGs received from territorial males: a group of 66 males came under attack 38 times (9.5 encounters/hour) by 14 different territorial males; the MG was under retreat and escaping for nearly two-thirds (64 percent) of the 2,900 m traveled during the four hours they were under observation.

Further insight into how territorial males treated different types of social groups during the defense of their territories was gained by comparing the frequency of intergroup aggressive types with each type of recipient social group (Figure 32). In their conflicts with neighboring PTFGs, PTFGs showed nearly equal proportions of chasing without entering the recipient group (Types I and II, 43 percent) and "passive" guarding of territorial borders (Types V and VI, 42 percent). Type VI was almost exclusively with neighboring territorial males when both males met at their mutual border without chasing, while non-neighboring MTFG males showed almost no inclination for such encounters. When interacting with Male Groups, the defending PTFG male most often ($P<0.005$) entered the group and chased individual males (50 percent of the time) without making contact with them (Type III).

PTFG males frequently chased away a trespassing MTFG without entering it (66 percent of the time) and only 16 percent of the time entered and chased individual members. Figure 32 indicates the type of aggression used by PTFG males in defending their territories and also the level of resistance by recipient groups. Movement toward, but not entering a MTFG was usually sufficient to force it away. This was not so for MGs. MGs had to be entered and individual members chased by the territorial male. MGs were less responsive

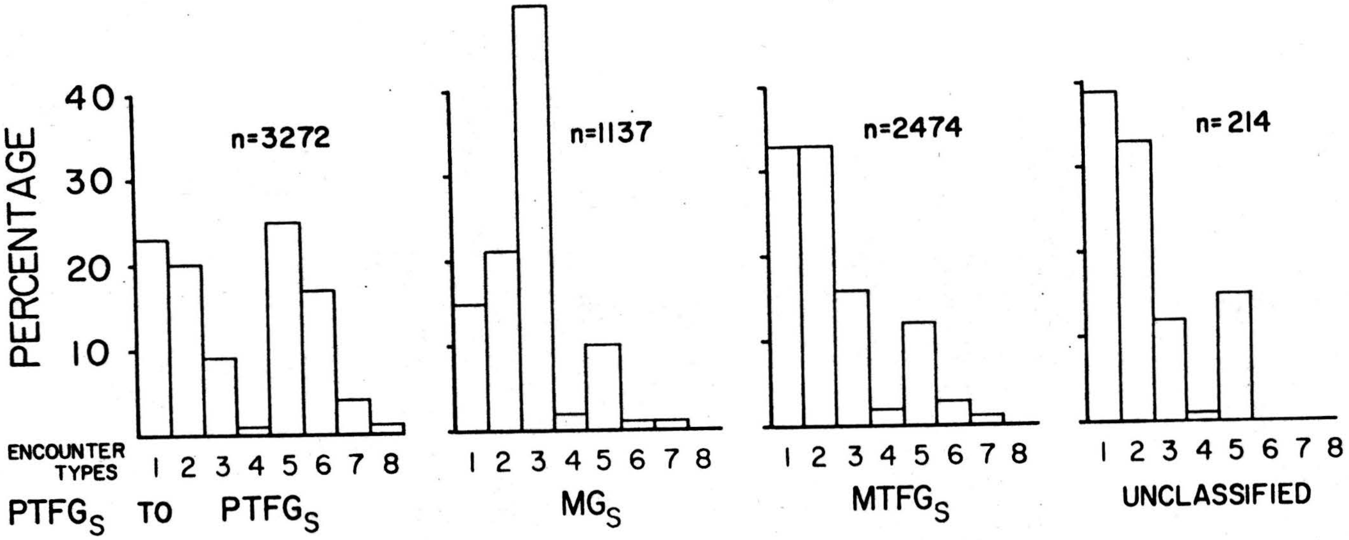

Figure 32. Proportion of intergroup territorial defense types initiated by Permanent Territorial Family Group males to other social groups.

and slower to retreat from attacking territorial males, probably because of their large group sizes. Attacks on male groups were typically short charges and circular chases within the group, while pursuit and chasing without entering the group was the most common form of attack against family groups.

Initiators and recipients of territorial defense

How often a male was involved in aggression with other males depended on a number of factors: (1) how often males and groups intruded upon the territory, (2) the number of neighboring males, and (3) the motivation of the given male to expand his own territory. Males might intrude upon a territory in an attempt to acquire part of it; they might be merely passing through the territory on the way to water or to feed; or they might be seeking to acquire females. Males were Initiators or Recipients of attacks depending upon the circumstances. There were in fact, large differences between males in the rates at which they initiated and received encounters (Table 7). Some males initiated far more encounters than they received and vice versa.

Marginal groups, that had to leave their feeding territories more often than PTFGs, were frequently the recipients of aggressive encounters when they trespassed onto other territories. For example, MTFGs 205 and 209 were strong Recipients (Table 8). Group 219, although considered a PTFG, was on a small near-marginal feeding territory. Because 219 often had to leave its feeding territory,

Table 7. Rates at which individual males defended their territories and rates their groups received aggression from other territorial males. Initiator Rate (IR) = number of encounters initiated by a male per 10 hours male was observed. Recipient Rate (RR) = number of encounters received by a group per 10 hours group was observed. May 1969 to April 1971. N = 2,251 encounters initiated and 2,399 encounters received.

Group Number	Number Of Three-Month Seasons Observed		Year One		Year Two	
	Year One	Year Two	IR	RR	IR	RR
205	4	4	0.7	0.9	0.7	1.7
207	4	1	0.9	1.3	1.8	0.9
208	4	4	1.4	1.6	1.9	1.5
209	4	4	1.4	1.6	1.8	2.7
211	4	4	3.3	1.3	2.7	1.5
212	4	4	1.0	1.0	1.8	1.2
213	2	0	1.9	0.9	--	--
214	4	0	1.8	1.2	--	--
215	4	4	1.3	0.5	1.9	1.2
216	4	4	0.9	1.5	1.1	1.2
217	4	2	0.4	0.4	0.4	0.8
219	4	4	0.9	2.2	1.2	2.5
227	4	4	2.1	3.0	1.6	1.7
228	2	4	2.6	2.4	2.1	0.7
229	1	4	1.3	4.3	2.2	2.3

the group was also a strong Recipient. Male 207 was a Recipient in Year One because he was less vigorous in defending his territory, more permissive in allowing outsiders to join and leave his group and because his unusually large group often left their feeding territory to water and feed. In contrast, group 211 male was an unusually strong Initiator because he vigorously defended his territory against trespassers and because his group infrequently left its territory to seek water or food. Seven out of the nine groups with territories in favorable habitat were Initiators. Groups 216 and 229 were the exceptions.

PTFG male 229 was a strong Recipient during the first 6 months when he first became a territorial male. An abnormally high number of his encounters (58 percent) were Types VI, VII and VIII, involving chasing and fighting with his neighbors, especially male 228. Once he was firmly established as a territorial male, 229 was a weak Initiator for six months from August 1970 to January 1971. But in February, March and April of 1971 he reverted back to a strong Recipient. In late April he lost his territory to a Solo Male and his adjacent neighbor 228.

Disturbance of family groups by male groups and solo males

The disturbance and disruption of family groups by Male Groups and Solo Males was associated with these outside males attempting to remove females from family groups. Male Groups entered and disturbed family groups chiefly in fall (58 percent) and secondarily in winter (25 percent). Usually when members of a male group entered a family group they appeared playful and curious. One or more of the larger and more dominant males of the group, however, often made serious attempts to chase and steal one or more females from the family group. But in only one out of 14 cases did an intruding MG succeed in removing a female from her group.

Solo Males that attempted to steal females from a family group normally had an established territory but no females. They were more persistent and aggressive than males from MGs. When SMs attempted to remove females from the group, the resident male vigorously defended his females. Long chases and hard fighting between the intruding male and the family group male resulted. SMs entered and disrupted family groups to secure females throughout the year, but most often in summer (40 percent). SMs succeeded in obtaining females one-fourth of the time in 20 attempts observed.

To a territorial male, the outside males were a threat of losing one or all of his females and his territory. Solo Males or Male Groups so badly disrupted a family group that in three cases, the territorial male permanently abandoned his territory or lost all his group members.

In early March 1970, male 214 permanently left his territory with one female and her cria after having lost two other females to a marauding MG and to a neighboring SM. Over a 1-week period in mid-March 1970, male 207 lost all seven of his adult females and their four crias to SMs; shortly thereafter, he permanently left his territory. Male 208 lost all four of his females to SMs in mid-March 1970, but stayed on his territory and eventually obtained an adult female and cria three months later.

Although the three cases were less than 8 percent of the 40 to 45 identifiable and established family groups under observation at one time or another during the study, the loss of territory or females meant the temporary or permanent loss of the males' participation in breeding.

Relations With Other Grazing Species

The Pampa Galeras region is a traditional grazing zone for herders from Puquio village. The small *criolla* breed of sheep (*Ovis domesticas*) (36 sheep/km^2) and alpaca (28 alpaca/km^2) were the most common domestic animals in the Cupitay Valley study area (Table 8). Domestic stock reached their highest densities in summer (105 animals/km^2) and lowest in spring (42 animals/km^2). Sheep fed on the slopes (51 vs. 19 percent) and flat (39 vs. 19 percent) more than alpaca ($P<0.01$), while alpaca showed a higher use ($P<0.01$) for the bottomland than sheep (43 vs. 10 percent). Alpaca highly preferred VT-7 (preference = 650), VT-15 (1,014) and VT-8 (2,130) on

Table 8. Mean seasonal densities of domestic animals in the Cupitay Valley study area from May 1969 to April 1971.

Domestic Animals	Total Animals Observed In All Scans	Animals/Km^2				
		Summer	Fall	Winter	Spring	Year-Round
Sheep	297,835	60	48	22	26	36
Alpaca	225,247	44	35	20	15	28
Llama	7,930	1	1	1	1	1

Table 9. Average year-round biomass of grazing ungulates in Cupitay Valley study area.

Species	Mean Density (No./Km^2)	Estimated Weight Per Animal (Kg)	Biomass (Kg/Km^2)	Percentage
Sheep	36	25	900	23
Alpaca	28	70	1960	50
Llama	1	95	95	2
Vicuna	20	50	1000	25

the bottomland. Llamas used the slopes 47 percent of the time, flat 31 percent and bottomland 20 percent; llamas used (23 percent) the tall-coarse bunch grass community (VT-11) more than the other grazing species. In Year One of the study, vicunas (n = 56,000) used the ridge 4 percent, bottomland 16 percent, flat 23 percent and the slopes 57 percent of the time. Vicunas made greater use of the ridge and slopes than domestic animals ($P<0.01$).

The total average biomass of grazing ungulates was 40 kg/ha with vicunas representing only 25 percent of the total (Table 10). Compared to the biomass of African ungulates (Hirst, 1975), total ungulate biomass in Cupitay Valley was 400 percent that of East African woodland and forest habitats, 80 percent of East African scrub savanna/semi-arid grasslands and South African woodland/savanna, and only 20 to 40 percent of East and Central African savanna grassland.

Vicunas usually did not defend their territories against other species. Alpacas and llamas often fed peaceably side by side with vicuna. They showed no sexual interest in each other. Twice, however, vicuna males chased domestic animal groups from their territories. In March 1970 male 207 vigorously attacked a herd of 80 alpaca, displacing them 50 m from his sleeping territory. On 27 April 1970 a flock of 550 sheep was grazing toward a vicuna family group. The vicuna male chased individual animals in the flock in an attempt to change their course of movement. Only after a half dozen separate attacks did the sheep change direction and retreat 100 m from the aggressive male vicuna.

People alone or with their domestic stock were responsible for nearly 90 percent of the disturbances observed (n = 1,712). The rate of disturbance was highest (1.0 disturbances/vicuna group/10 hours) during the growing season when the greatest number of domestic animals were present; and lowest (0.2 disturbances/vicuna group/10 hours) in the dry season when most herders had taken their domestic stock out of the Pampa Galeras region.

A vicuna family group commonly retreated from human disturbances that occurred within a few hundred meters of the group. Invariably, the vicuna group would return to its regular daily pattern of activity within an hour or so. Escape was usually uphill in the direction of the group's sleeping territory. If the disturbance occurred in the late afternoon they continued moving to their sleeping territory for the night and returned to their feeding territory the following morning as usual.

Feeding and Sleeping Territories

Permanently established vicuna family groups occupied year-round feeding and sleeping territories. The feeding territory was located on a lower slope, flat or bottomland in good habitat, while the sleeping territory was on some nearby flattened ridge which separated the broad valleys. The sleeping territory was in an area of poor to fair habitat.

Territorial borders were well defined and rigorously defended by the occupant male (Figure 33). The 1 to 3 m wide boundaries that

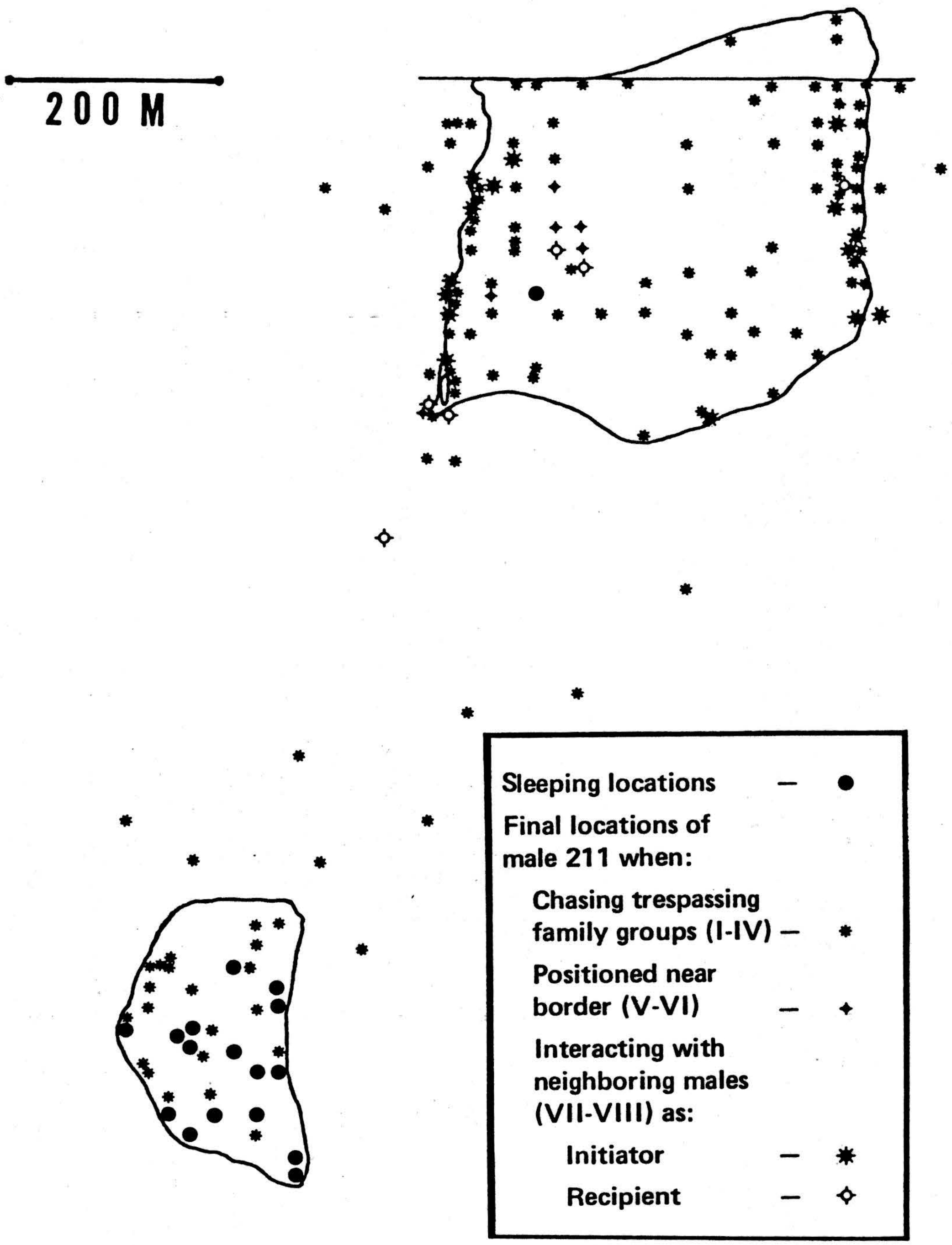

Figure 33. Defense of feeding and sleeping territories by male 211 and locations where family group slept in spring 1971. Intergroup aggressive encounter types given as Roman numerals in key.

separated territories, while not visible to an observer, were clearly defined and learned by the resident family groups. Two adjacent family groups often fed tranquilly side by side only a few meters apart, each on its side of their mutual territorial boundary. If one group wandered across the border, it was promptly chased back to its own territory by the other group's male. Some territorial boundaries conformed to natural topographical features such as streams and gullies or man-made structures such as roads. A few groups seemed to use my rock cairns as visual landmarks for boundaries. Koford (1957) also reported that vicuna territorial boundaries occasionally followed natural and man-made configurations.

Sleeping territories

Most family groups passed the night on the ridge in their sleeping territory. A number of small sleeping territories clustered together formed a communal sleeping area. The one communal sleeping ground within the study area contained 7 to 10 sleeping territories on the south ridge (Figure 34). The remaining family groups in Cupitay Valley used other sleeping areas on ridges outside the study area. Communal sleeping areas were believed to be in short supply, since there were only 3 to 4 areas available for the 60-odd groups using the entire upper Cupitay Valley (20 km^2). Male groups did not share communal sleeping grounds with family groups. Family groups of the non-territorial plains zebra (Equus quagga) also come together at night on a common sleeping ground (Klingel, 1969).

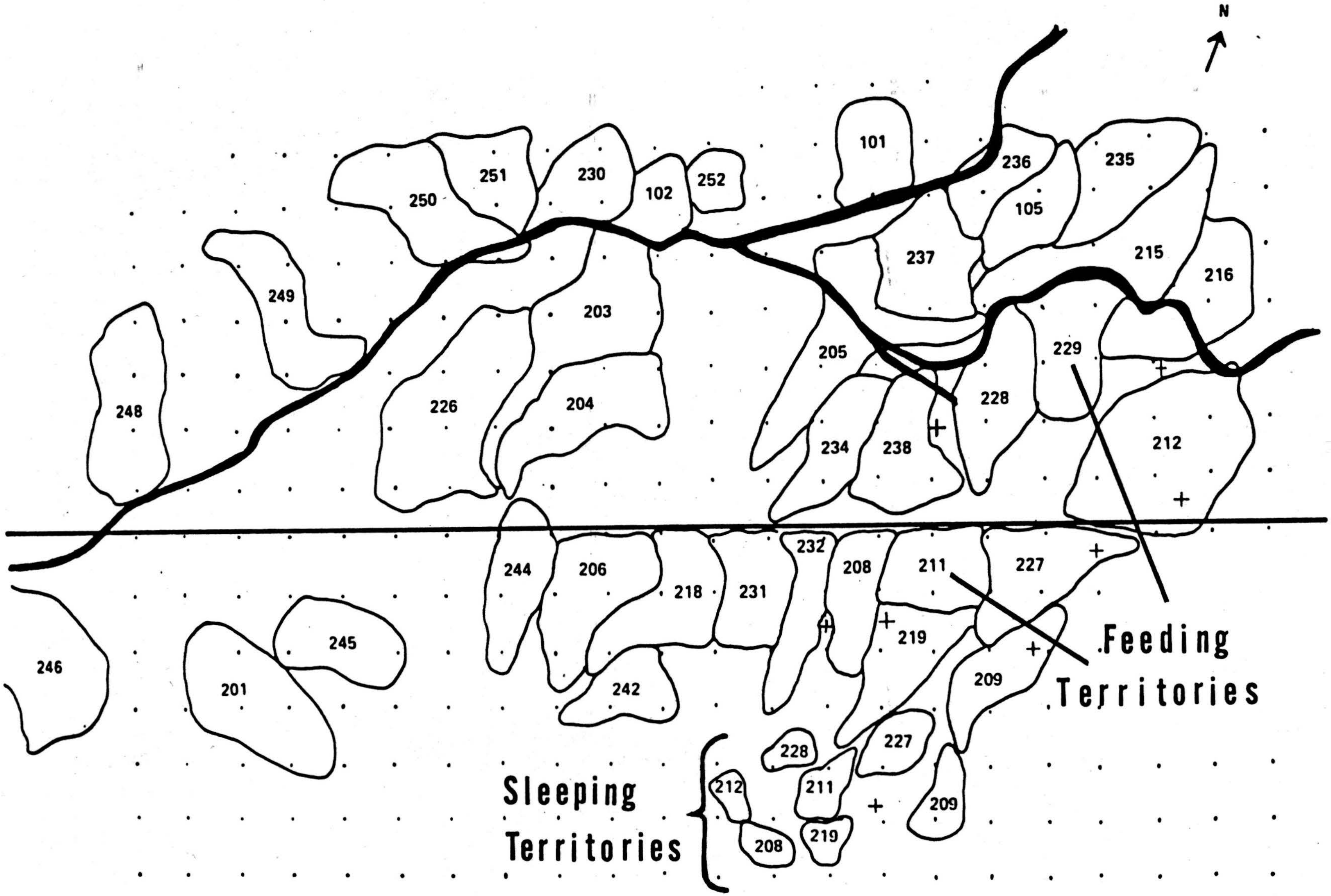

Figure 34. Size, distribution and shape of vicuna feeding and sleeping territories during the month of October 1970, Cupitay Valley study area.

The size of sleeping territories was determined by the area defended around where groups consistently slept (Figure 33). Sleeping territories averaged 2.6 ha in size (n = 43, S.D. = 1.4) and decreased insignificantly from Year One (2.8 ha) to Year Two (2.3 ha).

All vicuna groups with feeding territories on the slopes and most groups with territories on the upper flat, rarely slept there, but passed the night about 1 km away on the ridge. However, some groups on the lower flat and bottomland frequently slept on the upper flat, 200 to 400 m uphill from the center of their feeding territory, either just inside or slightly out of it. Family groups 203, 204 and 226 at the western end of the study area in Zone II usually (87 percent of 206 observations) passed the night next to each other on the upper flat where their three territories came together (Figure 34). Some groups (212, 213-228 and 214-229) on the bottomland and flat in Zone I also slept on the flat (52 percent of 454 observations) and in close proximity to each other. These groups showed a decrease to 27 percent of overnighting on the flat during the months of November, December and January. Possibly this shift was related to the birth season and increased hunting activity of the Andean fox.

Sleeping on higher ground offered several possible advantages over sleeping lower down: ridges were 7°C warmer than the bottomland in winter; by sleeping close together groups had a higher probability of detecting predators; and they avoided the stream bed gullies where predators commonly hunted. But there were also disadvantages for groups with two territories. The defense of two separate areas, daily movements back and forth between two territories and increased exposure to territorial males during these movements represented added energy costs. The prevalent behavior of maintaining two separate territories suggested that the advantages outweighed the disadvantages.

Daily movements between territories

At first light in the morning an observer could see numerous groups clustered together at the communal sleeping ground on the ridge, while the valley contained few to no groups. Groups began to move about in their sleeping territory a half hour before sunup. Animals slept within a few meters of a dung pile and the associated excrement influenced vegetation. As the animals arose, each walked to the nearby dung pile to defecate and began feeding. Within an hour after sunrise the group, led by its male, left its bedding area and walked downhill to its feeding territory, usually through a neutral corridor between territories of other groups. Group males were tolerant of other family groups in the neutral corridor, especially those whose sleeping territories were next to their own. Several family groups might feed and slowly walk near each other on their way to their feeding territories without intermixing. On one such occasion, five groups (including 211 and 212) totaling 42 animals were within 50 to 200 m of each other on an area only 2 ha in size. Twenty-five minutes later as the groups parted and moved toward their respective territories, male 211 chased group 212 400 m downhill because group 212 had entered 211's territory on its way to its own feeding territory. Only minutes before the two groups had been walking compatibly side by side.

A group spent most of the day within its feeding territory, except when disturbed or when the group left for water. In late afternoon or early evening the groups returned to their sleeping territories (Figure 35).

Distribution and spacing of feeding territories

Feeding territories were common on the flats, bottomlands and at the base of slopes. Flats and upper slopes dominated by the tall perennial bunch grass communities and long gradual slopes without water supported few feeding territories; such unoccupied zones accounted for the vacant areas shown in Figure 34. Vegetation types with moist deep soils at the base of shorter and steeper slopes were favored sites for feeding territories, especially if the site had immediate access to water.

Springs on the slopes were located between two or more feeding territories or just within the border of a single territory. Heavily used springs on the flat were often sandwiched in between territories in an undefended neutral zone. The territories of family groups 208, 211, and 219 convened at one spring. In some seasons the spring appeared to be within one territory or the other (Figure 34), but most often it was in a neutral zone or on a mutual border. It was not uncommon to see male 211 prevent other groups, especially unfamiliar groups from marginal areas, from watering at the spring. Yet since the spring was in a far corner of 211's territory, other

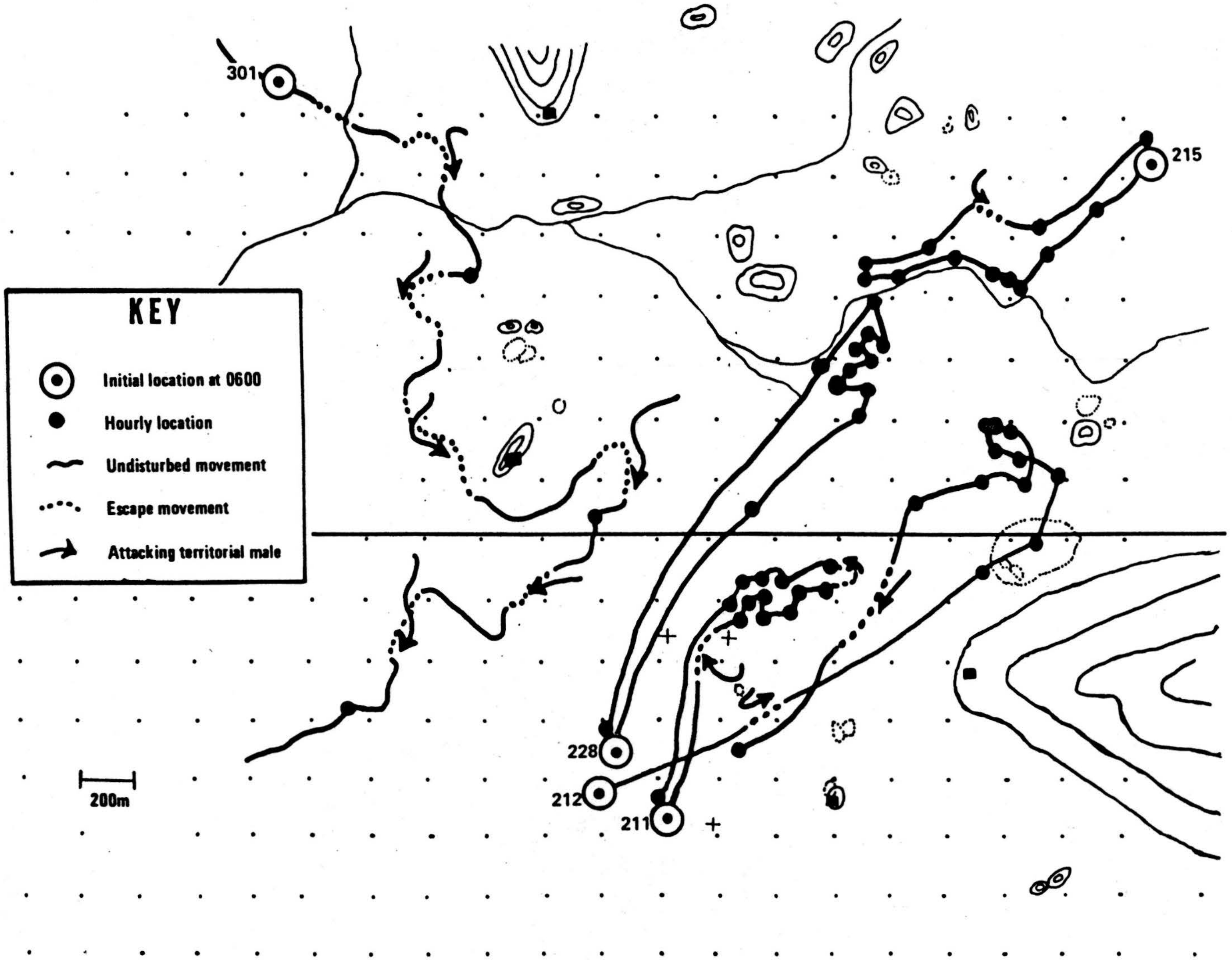

Figure 35. Typical daily movements of four selected PTFGs (211, 212, 215 and 228) and a MG (301) in the Cupitay Valley study area.

groups commonly managed briefly to water before being noticed and chased away.

Small gaps and narrow corridors opened up between some territories, especially in the dry season to allow outside groups access to water. MTFGs persistently seeking water apparently made these sites uneconomical to defend. Neutral spaces and corridors were especially conspicuous between territories 205 and 228, and 229, 216 and 212 (Figure 34).

When family groups moved onto the flat and bottomland during the dry season to drink from springs and the river, adult males were tolerant of other groups. This lack of aggression occurred because groups were off their own territories and in neutral zones not occupied or defended by any territorial family group male. Waterbuck (Kobus defassa) also have neutral zones between territories and water and show reduced aggression around watering sites (Spinage, 1969).

Family groups temporarily visiting neutral zones commonly came together to drink or feed side by side without mixing. Such large aggregations of as many as 50 to 80 animals sometimes appeared as one large group. Although crias from various groups often played together between and within groups other than their own, the adult females did not intermingle. Adult males prevented intermixing by standing between their own and the adjacent group. Males often made low intensity threats or short charges toward females of an adjacent group. If aggression became intense between family group males in neutral zones, some males were consistently dominant over others.

Size of feeding territories

Feeding territories varied in size from 1.9 to 55.8 ha and averaged 18.4 ha (n = 98, S.D. = 10.8). The size of feeding territories decreased insignificantly (6 percent) from Year One (19.0 ha) to Year Two (17.8 ha) as the density of groups increased. Territories remained in the same basic location from one season to the next, while their size and shape changed slightly (Figure 36). Except for group 207, groups with feeding territories at the base of the south slope had the least variation in size (S.D. = 2.6 ha) and groups on the flat and bottomland the most variation (S.D. = 6.2 ha). The territory size of the unusually large group 207 fluctuated most during the first year. Group 207's territory temporarily expanded onto the flat in the third season (spring) with the disappearance of group 213. The territory of group 205 changed greatly each season during the second year. It was mostly poor habitat and had high use by alpaca and sheep.

The shapes of territories were occasionally circular but frequently oblong to linear. Territory 215 was especially intriguing for its long narrow shape, an inefficient form to defend since the male had to move long distances to defend both ends. Group 209 differed from most groups by not having separate feeding and sleeping territories, but one continuous site on the ridge and upper slope.

Territorial exclusiveness

Neighboring PTFGs overlapped very little in their use of space (Figure 37). Territories were sharply separated and exclusively

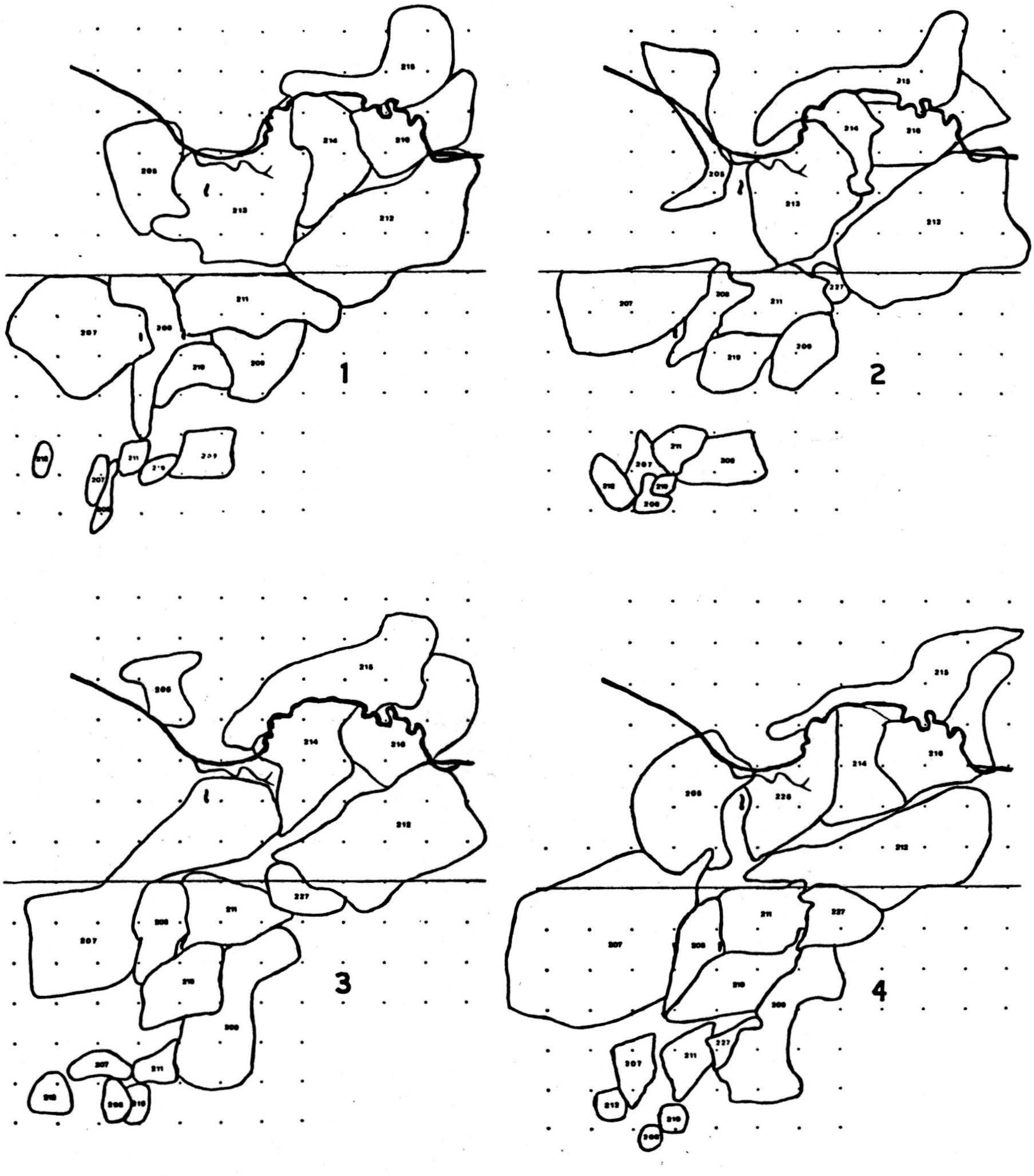

Figure 36. Seasonal changes in size, shape and location of vicuna territories over two years. Small circles at bottom of each map are sleeping territories, others are feeding territories. May 1969 to April 1971 (fall = 1 and 5, winter = 2 and 6, spring = 3 and 7, summer = 4 and 8).

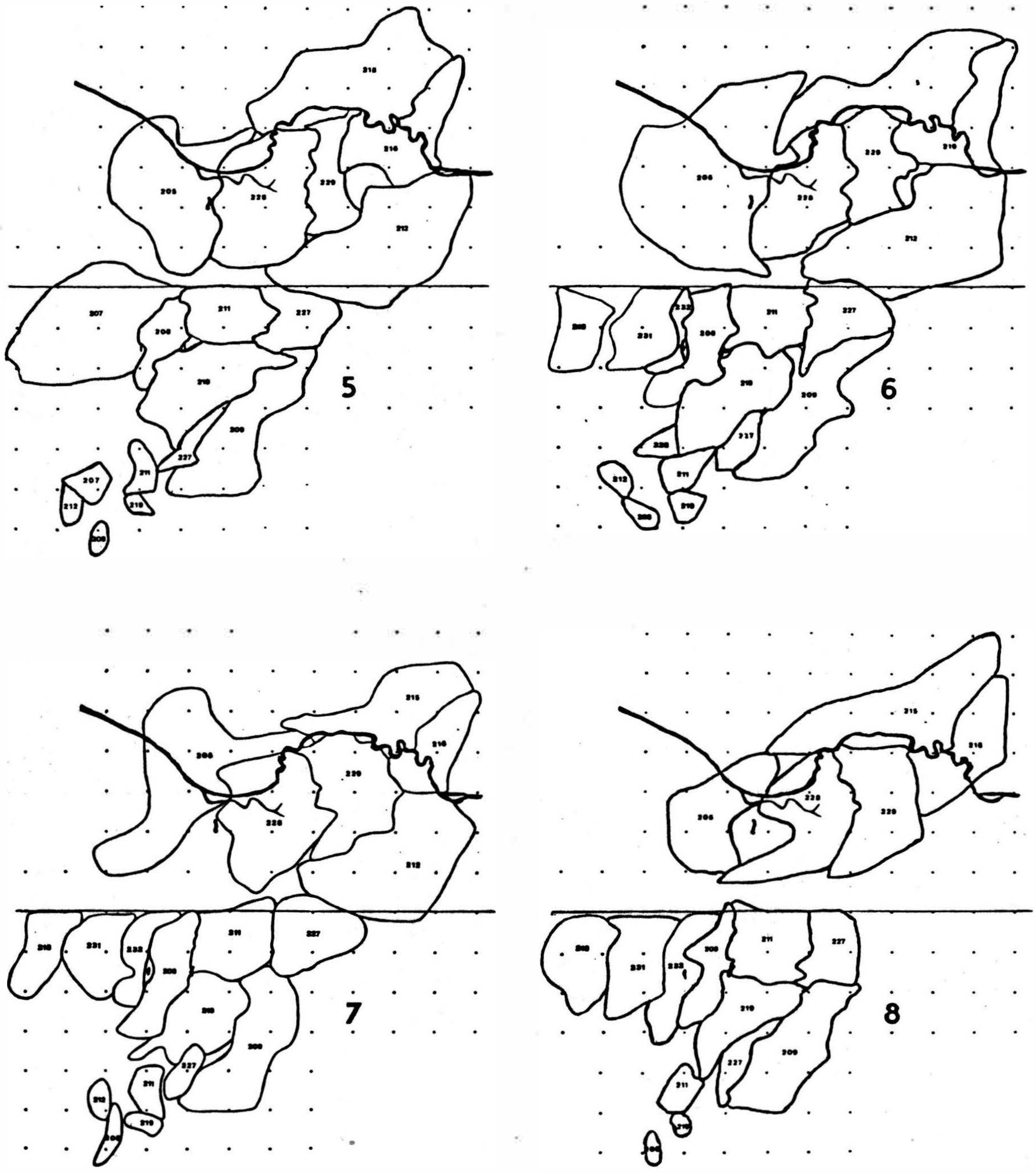

Figure 36. Continued.

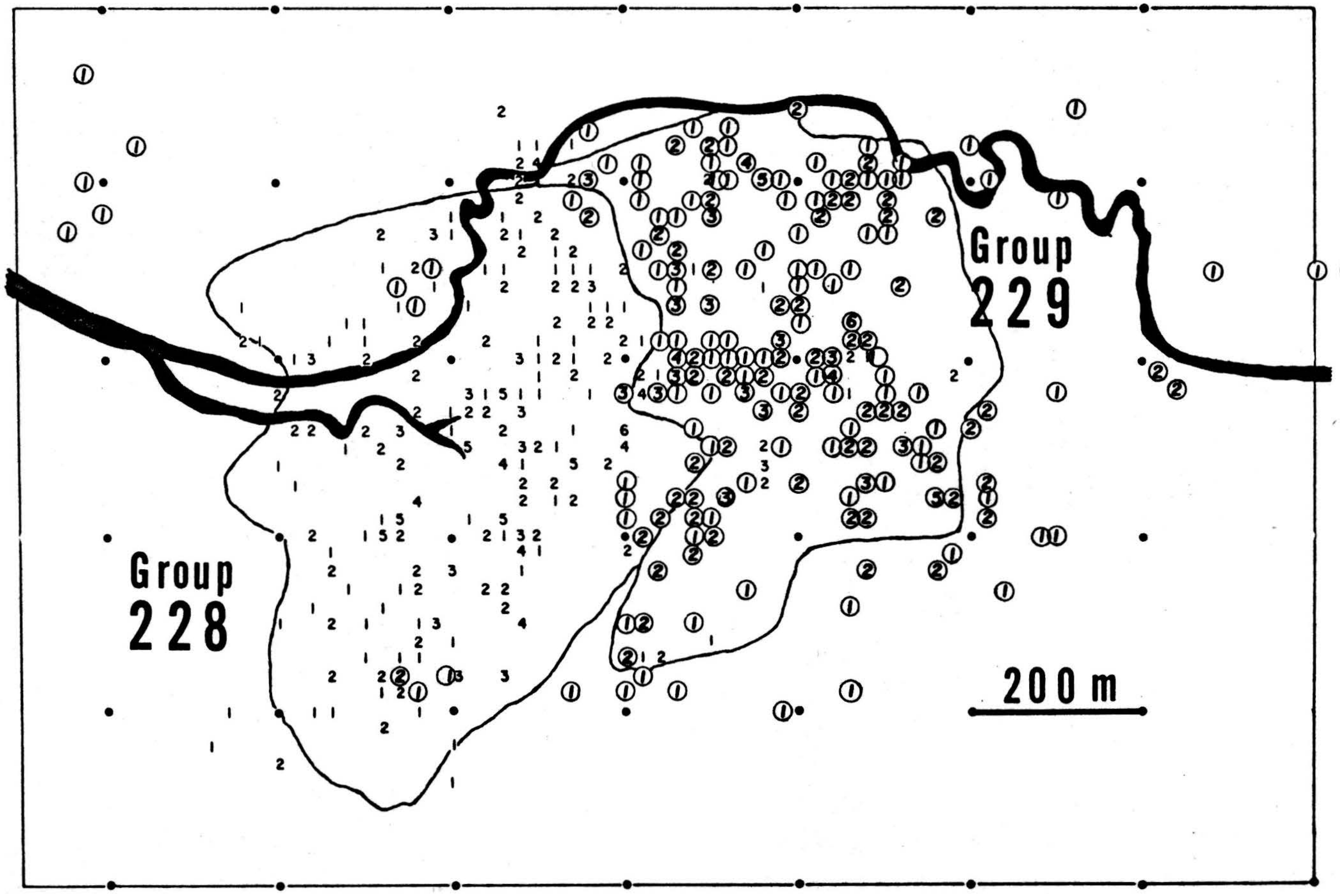

Figure 37. The location and number of hourly observations plotted at 20 m intervals illustrating the small degree of overlap between two neighboring PTFGs. Territorial boundaries drawn separately and based upon aggressive encounters between adjacent males. Spring 1970-71.

occupied. However, MTFGs coming into the area to water or feed in neutral zones would flagrantly violate the exclusiveness of a territory if the resident group was absent. Such non-neighboring groups might enter an unoccupied territory to feed for a few minutes to several hours until they left or the resident male returned and chased them away. While family groups were absent from their sleeping territories in the day, wandering MTFGs occasionally stopped and grazed in the communal sleeping ground belonging to other groups.

For example on 16 July 1969 PTFG 205 was absent from its feeding territory. Four MTFGs and a MG that came onto the flat during the course of the day to water stayed in 205's territory for several hours. One day in late October of 1970, PTFG 231 didn't come to its feeding territory and four outside groups stopped to feed during the morning. The adjacent 232 male didn't influence them except to prevent their entering his own territory.

When a group was temporarily absent from its territory, the adjacent groups normally did not enter the unoccupied territory. If they did, it was only briefly. For example, on 15 July 1969 four groups (207, 209, 211 and 401) fed close to one another for about 2 hours within the territory of 227 while it was absent. Once in mid-September 1969 while group 208 was absent from its territory and on the flat, neighboring group 219 moved into 208's territory to feed. When 208 returned, the male immediately chased the 219 females from his territory as male 219 stood by and watched.

Three important points emerged from these observations on territorial exclusiveness: (1) regular occupancy was necessary for exclusive use and continued ownership of a territory, (2) territorial exclusiveness was not honored by outsiders coming upon a vacant territory, and (3) neighbors rarely moved into an adjacent territory when the resident was absent.

Restrictions of feeding use as a result of territorial behavior

When the study began I arbitrarily distinguished between PTFGs and MTFGs based upon the relative quality of habitat. Later analysis of vegetative types bore this out. PTFGs occupied the best sites with better access to permanent water and higher percentages of preferred vegetation types than MTFGs (Table 10). Counts of surface area units showed that PTFGs had a higher proportion of VTs 1, 3, 14, 6, 8, 7, 12 and 13 than MTFGs, while MTFGs had higher proportions of the poor VTs 4, 2, 10 and 11 (Chi Square = 6.82, D.F. = 1, $P<.01$).

What vicuna fed upon was dependent on access to vegetation types and access was determined by the relative status of different social groups. MGs and MTFGs had lower social status than PTFGs. MGs and MTFGs used the common and non-preferred bunch grass communities (VT-4 and VT-11) 1.7 times more than PTFGs ($P < 0.10$ for VT-11). MGs had to rely on the non-preferred VT-2 more than other social groups ($P < 0.10$). In contrast, PTFGs fed on the highly preferred and high producing VT-1 ($P < 0.01$) and VT-3 ($P < 0.10$) more than MGs

Table 10. Comparison of vegetation types in territories of MTFGs and PTFGs. Spring 1970-71. Good to poor vegetation types based upon preference, plant species composition and production of palatable species.

	Vegetation Types	Percentage Of Territories In Vegetation Type			
		MTFGs	PTFGs		
		209&219	208&211	215&216	228&229
Good	1	1	3	7	5
	3 & 14	9	22	33	6
	6	0	0	1	7
	8	0	0	5	40
	7	0	0	4	0
to	12	0	0	6	4
	13	0	1	2	0
	4	11	23	5	7
	2	34	39	36	31
	10	11	0	0	0
Poor	11	34	12	0	0
TOTAL		100	100	100	100
Hectares		31.6	22.7	36.3	40.0
Source Of Water		Semi- or Permanent Spring	Permanent Spring	Stream	Stream

and MTFGs (Figure 38). PTFGs also made the greatest feeding use of the highly preferred VT-8.

VT-1 received its greatest use during the summer, especially by PTFGs, when the plant growing and birth seasons occurred. VT-3 that was located on the moist to wet soil types on the lower slopes, had peaks of high use by most social groups in the dry winter. MGs and MTFGs used the coarse bunch grass dominated communities (VT-4 and VT-11) particularly in the winter and spring, while MTFGs used the riparian community (VT-9) more than other social groups in connection with their visits to the river for drinking water. VT-6, the year-round green and marshy community, was most important to vicuna during winter when other vegetation had completely dried out and available forage was low.

During the second year of the study when total density and the number of territorial family groups was higher, feeding use of vegetation types did not necessarily increase proportionally for all social groups, but MGs had to go to other types less preferred by family groups. VT-2 received 17 percent more use in the second year than the first year by all social groups, with the greatest increase (24 percent) for MGs.

Effects of habitat quality and season upon territory use

Habitat quality greatly influenced how much time a vicuna family group spent within its feeding territory. For purposes of analysis, home range was defined as the feeding territory, sleeping territory

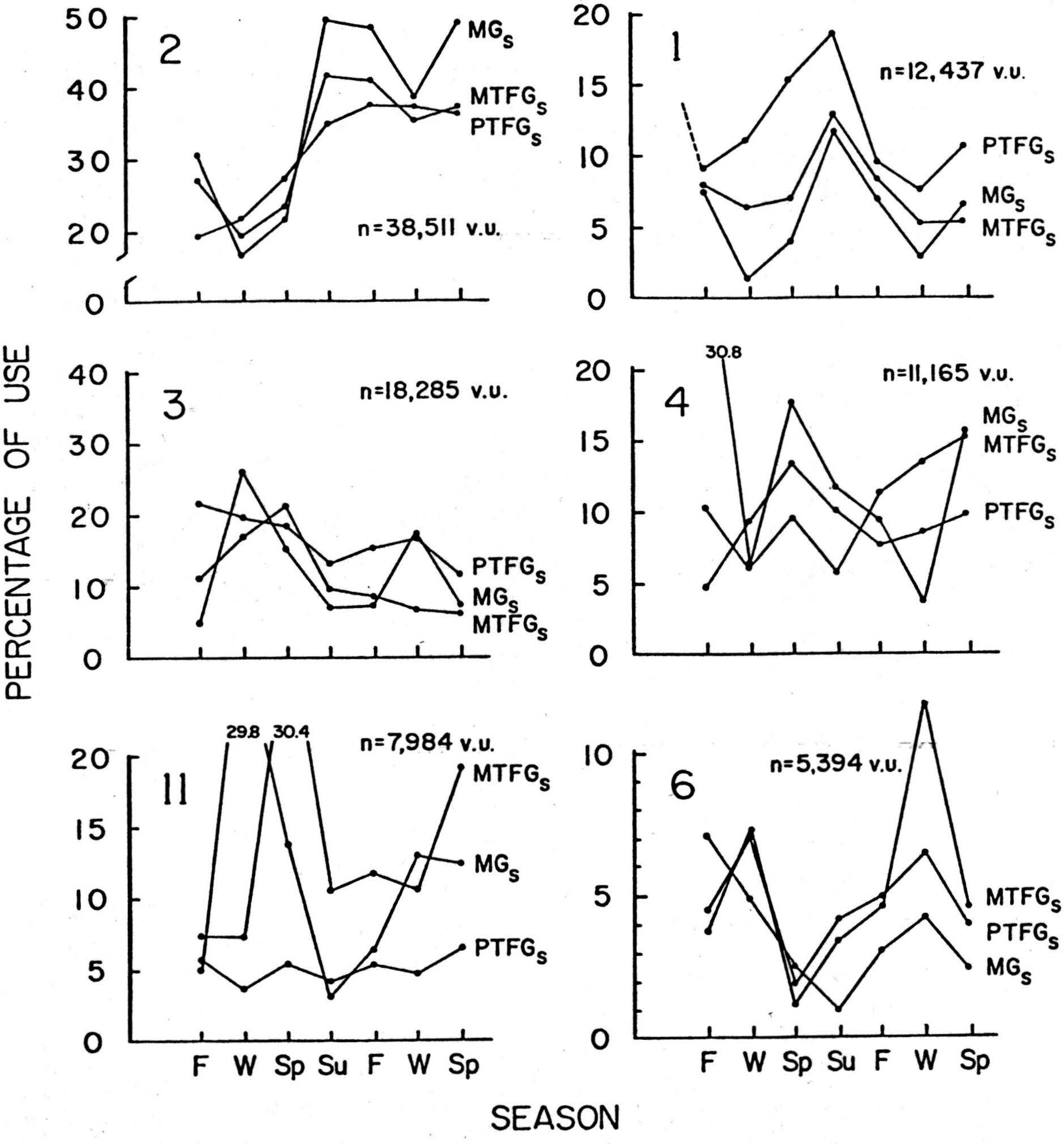

Figure 38. Seasonal changes in feeding use by vicuna social groups of vegetation types 2, 1, 3, 4, 11 and 6.

and connecting corridor; excluded were travel routes to water outside the home range and temporary use of territorial space of other groups. The percentage of daylight hours family groups spent within their home range was determined by the topographical location of their feeding territory, access to permanent water and the abundance of preferred vegetation types within the feeding territory. Family groups on the bottomland with a high percentage of preferred vegetation types and immediate access to the river, spent 85 percent of the time within their feeding territory (Figure 39). Family groups on the ridge and upper slope with only close or immediate access to springs and a low percentage of preferred forage types spent 39 percent of the time within their feeding territory. Groups in poor habitat also spent more time in their sleeping territory, moved more slowly between their two territories and were outside their home range more than groups in better habitat. Thus, the more favorable the habitat, the more time a family group spent within its feeding territory.

The seasonal variation of territorial use for 10 groups occupying a gradient of habitat types is given in Figure 40. In the first year groups were in their feeding territories most often in summer (73 percent) when forage was abundant and least often in spring (54 percent) when forage and water were scarce. Converse to the progressive decline of territorial use from fall to spring, there was an increase of time in sleeping territories and between sleeping territories and feeding territories.

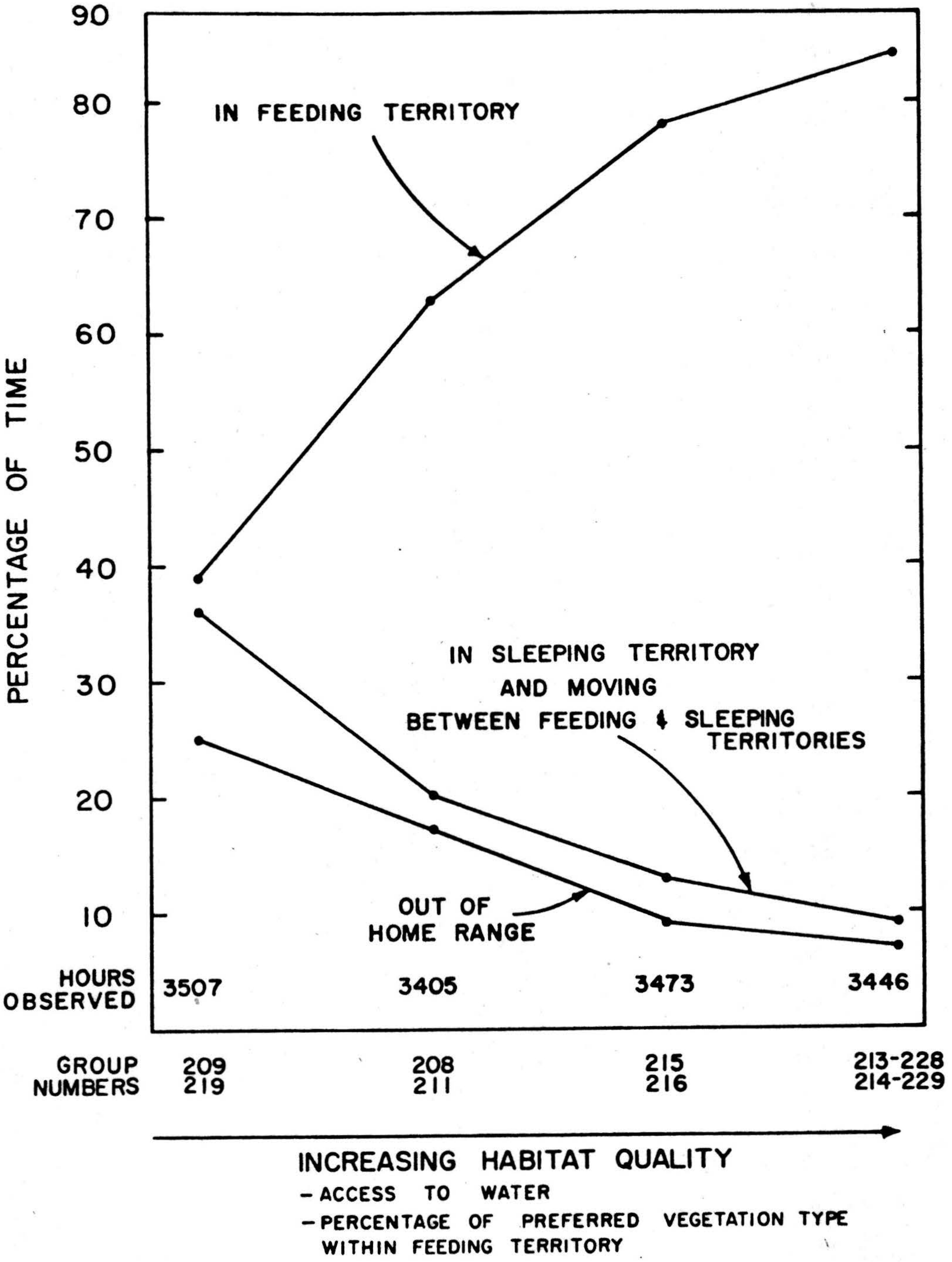

Figure 39. The relationship between habitat quality and time spent in feeding territory and outside of home range.

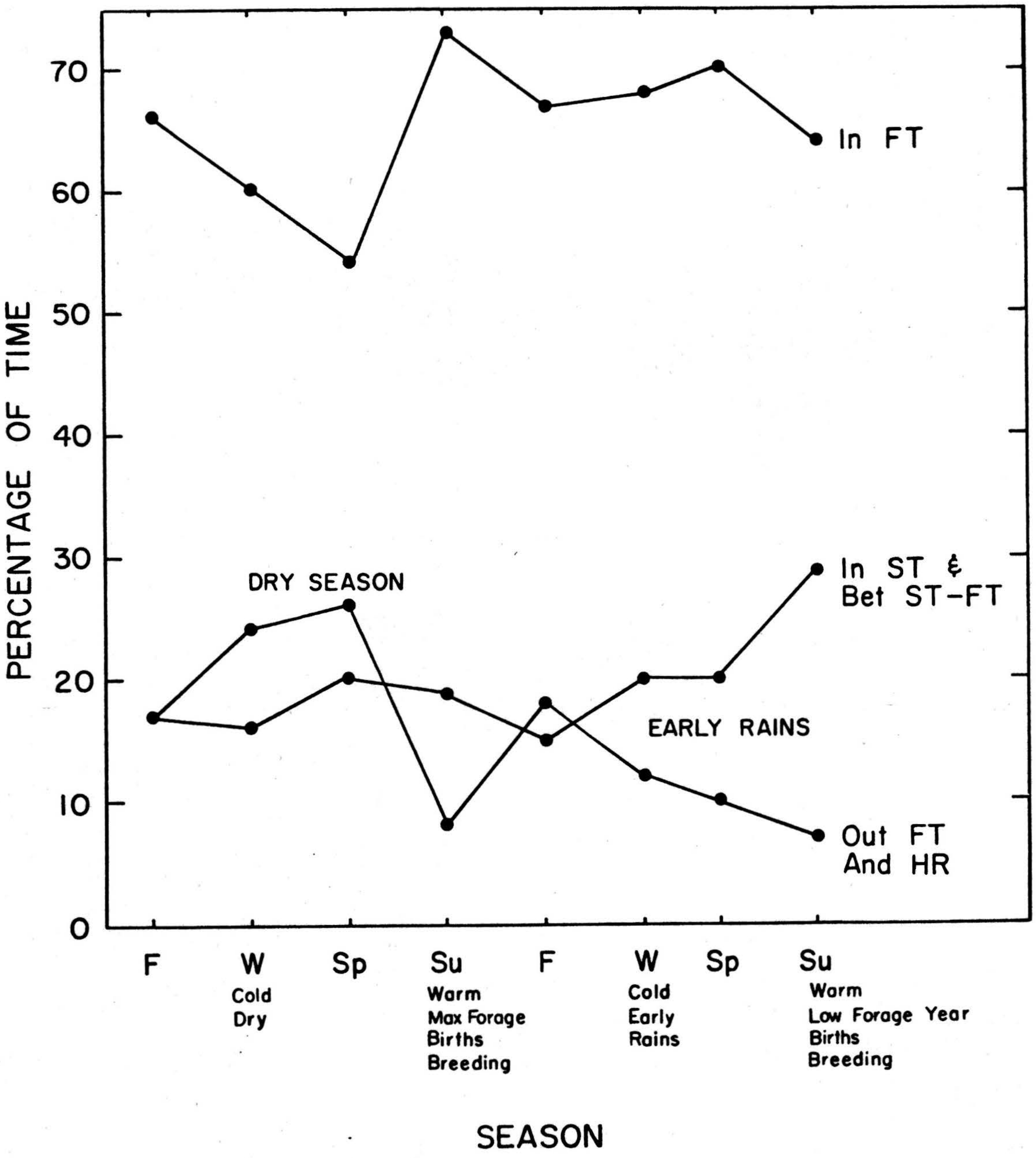

Figure 40. Percentage of time groups were within and outside their home ranges as related to time of year.

In the second year groups spent more time in feeding territories and less outside their home ranges due to a long growing season and early winter and spring rains. The long and productive 1970 summer continued to provide forage into the following fall and winter; the reverse had occurred the previous year when it was preceded by the short growing season of 1969. Rains during the normally dry season also provided drinking water in spring. Groups were outside their home ranges least often during summer for both years.

MTFGs on the ridges and upper slopes temporarily left their feeding territories and home ranges almost daily during the winter. Even some PTFGs on the slope and upper flat were absent from their home ranges. When they did leave, they departed from their feeding territory between 0800 and 1130 and returned between 1330 and 1700; they were absent an average of 6 hours (1-10, n = 69).

Family groups left their home ranges primarily to drink, although they also fed while absent. Routes of travel were directly to a source of water. Sudden and abundant rainfall during the late dry season resulted in a sharp decrease of MTFGs using the flat and bottomland. For example, on 4 February 1971 12 MTFGs totaling 53 animals visited Zone I; 1 week later during the morning, five MTFGs totaling 20 animals were there before a hard rain started and continued into the night. The next day only one MTFG descended to the flat to water. Long movements from home ranges fluctuated with monthly rains for most groups, but some continued to leave even after the beginning of the rainy season. These were groups with poor feeding territories that needed to feed on other sites. When the growing season began, they too discontinued leaving their home ranges.

In the late dry season, groups outside their home ranges were noticeably more reactive and flighty. Disturbances from sheep herders or horsemen sometimes suddenly triggered en masse retreats of five to ten groups running from the valley floor towards the ridge.

Relationship between group size, territory size and forage productivity

Koford (1957) reported that where forage was sparse and coarse, territories were large, but they were small where forage was relatively abundant and succulent. The same was observed in this study, but larger territories also contained more animals. In both years there was a significant correlation between mean group size and mean territory size (Figure 41). Groups 213 and 228, that occupied the same site at different times, were not included because domestic animals intensively fed in their territory.

Seasonal correlations between group and territory size for two years were $r = 0.44$ (no significance) during fall, $r = 0.48$ ($P<0.05$) in winter, $r = 0.72$ ($P<0.01$) in spring and $r = 0.77$ ($P<0.01$) in summer. The highest correlations occurred during critical seasons: spring when forage was minimum and females were in the final phase of

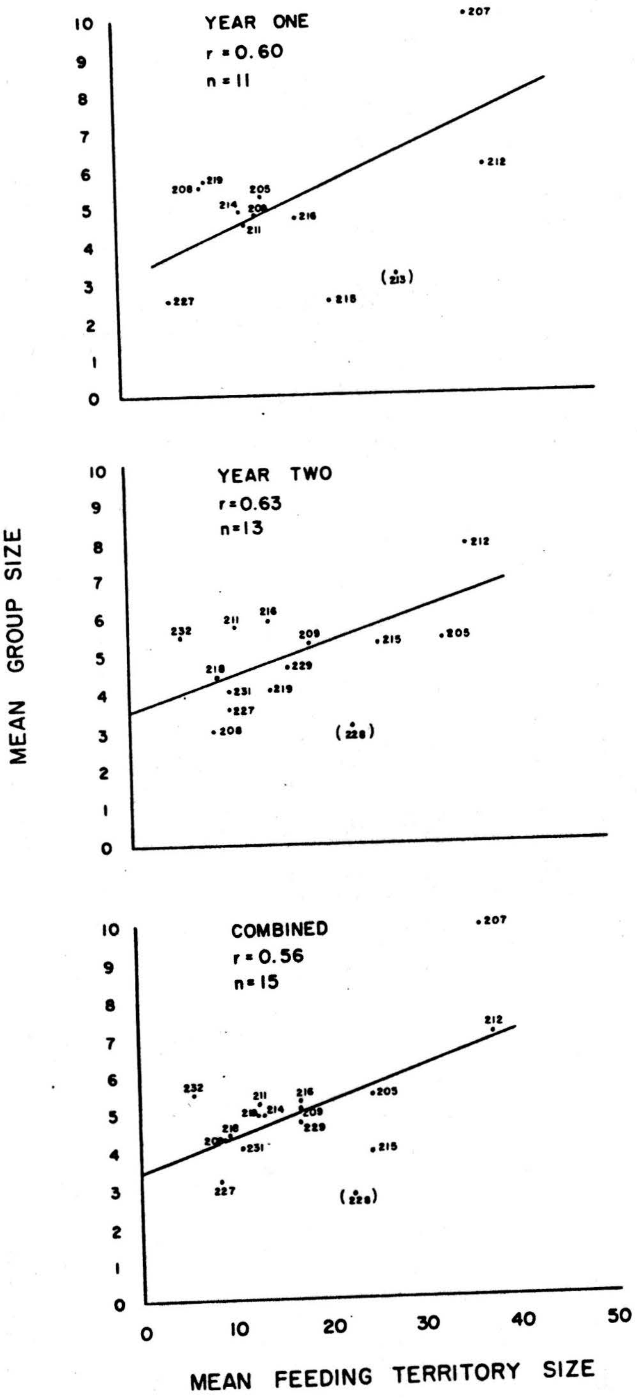

Figure 41. Correlation between group and territory size ($P<0.05$).

gestation, and summer when, although forage was maximum, energy demands were high for birth and lactation.

A primary question of this study was whether the numbers of animals in feeding territories were in balance with their food resources. If a relationship existed, it would be expected to be especially obvious during spring when forage conditions were poorest. In the spring of 1970 mean group size and total forage production were highly correlated ($r = 0.86$, $P<.01$) for 12 of 14 groups examined (Figure 42). The feeding territories of groups 205 and 228 were excluded from the analysis. They contained unusually high amounts of VTs-7, 8 or 15 that were highly preferred and used by alpaca and sheep. The relationship between group size and territory size was nearly the same as between group size and forage production. Forage production and territory size were highly related ($r = 0.98$, $P<.01$) in spite of the great differences in production between vegetation types. The high correlation between total forage and territory size suggested a uniform habitat, that was in fact highly variable. The variation in production of vegetation types was compensated for by their patchy distribution, causing common types to occur in most territories and in average proportion to their availability. In spite of the wide variation in the relative proportion of vegetation types found within territories, 60 percent of territories were types with similar production (2, 4, 8 and 13). Thus, similar production per unit area within territories resulted from a high percentage of similarly producing vegetation types.

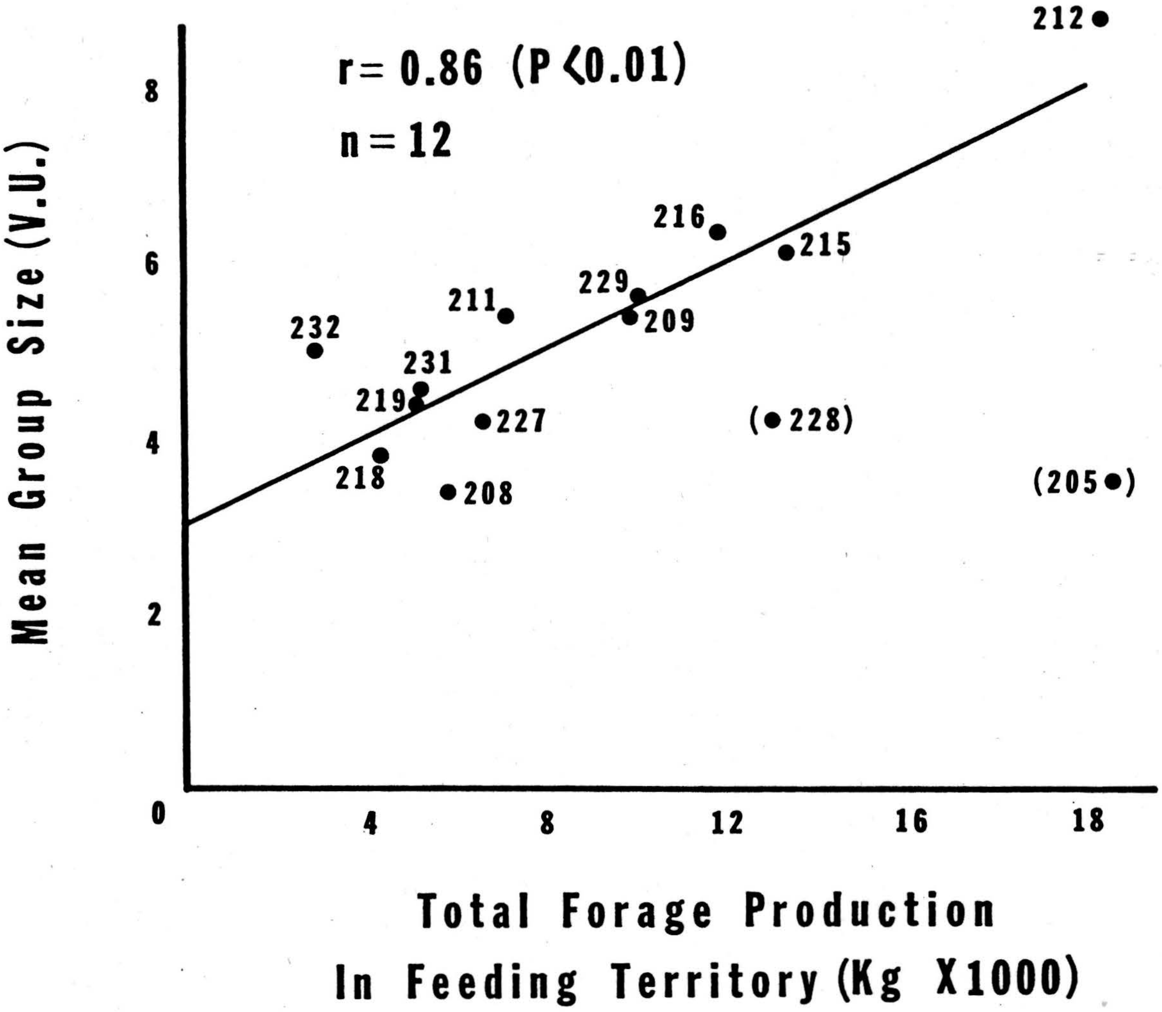

Figure 42. The amount of forage produced in feeding territories compared to number of vicuna units in each group, spring 1970.

Average available forage production within all territories was 550 kg/ha (S.D. = 70) compared to 630 kg/ha (S.D. = 300) for the entire study area. Production within territories varied with location and conditions. Production was lowest (456 kg/ha) in territories on dry upper slopes and ridges; intermediate (532 kg/ha) on the bottomland, flat and dry slopes; and highest (642 kg/ha) in territories on moist lower slopes with relatively high proportions of vegetation types 1, 3 and 14. Excluding groups 205 and 228, the amount of forage in territories per animals ranged from 533 to 2,226 kg/vicuna unit and averaged 1,546 kg/v.u. (S.D. = 490).

Thus it appeared that the numbers of vicuna using a feeding territory was related to both the size of the territory and total forage within it. That such a relationship existed despite the heavy use of the area by domestic animals suggested that vicuna also adjust their numbers in a family group to compensate for this use.

Family Group Integration

Establishment of a territory

Males that had reached sexual and physical maturity and were ready to establish a territory left their Male Groups and became Solo Males. The larger males which dominated other males in MGs were suspected to be those who left and became Solo Males. Some males left their MGs accompanied by one to several other mature males.

While making my routine observations within the study area, my attention was often drawn to the arrival of a Solo Male. His constant and erratic movement gave the impression he was confronting established territorial males to probe for areas poorly defended or unoccupied. These males were a threat to an established territorial male. Mature SMs, especially when accompanied by several others, were quickly attacked by local territory owners. On 26 May 1970 I observed a group of 7 large males from 0805 to 1154. During this time eight different territorial males chased them out of one territory to another for a total of 18 separate chases. The group of males was in retreat for three-fourths of the 4,000 m they traveled in this time.

A male became territorial by several methods. Most common of these methods was to establish himself on a suitable unoccupied site or abandoned territory. If a SM discovered a likely location during his constant movements and was not driven away by neighboring territorial males, he would remain. The newcomer spent most of his time in the beginning feeding and resting; only occasionally did he challenge neighboring males. This relatively non-aggressive period lasted as long as 7 months before a male had fully established himself on his territory. Gradually the male became more involved in aggressive encounters while testing and learning the limits of his newly claimed territory until he initiated more territorial defenses than he and his group received (Table 11).

Complete sequences of males 227, 228 and 229 establishing their territories was obtained. The adjacent SMs 228 and 229 fought frequently over their common border, resulting in a high percentage of high intensity intergroup Encounter Types VI, VII and VIII; 43 percent of male 228's encounters during his first 3 months and 57 percent of 229's encounters during his first 8 months were one of these

Table 11. The number of intergroup aggressive encounters initiated (IR) and received (RR) per 10 hours by males when establishing their territories. Total hours three males observed equals 3,059.

	Group Number		
	227	228	229
Season	IR - RR	IR - RR	IR - RR
Winter	0.0 - 7.4	-	-
Spring	1.0 - 2.5	0.0 - 1.7	-
Summer	2.9 - 2.7	2.7 - 2.4	1.3 - 4.3
Fall	2.3 - 1.7	3.8 - 0.7	1.8 - 3.9
Winter	1.6 - 1.4	1.7 - 0.6	2.4 - 1.5

three types. The two were observed chasing and fighting each other over several kilometers across the Pampa, far beyond the confines of their territories during this period. In contrast, for MFG male 227 that did not establish himself adjacent to another new territorial male, only 23 percent of encounters in the first 6 months were Types VI to VIII.

I observed 10 SMs successfully establish territories. Seventy percent of these first took up residency in their new territories during late January or early February; the others became established in March, April and August. In one instance, two large males amiably traveling together, eventually became SMs and established adjacent territories and were then aggressive towards each other.

The second way to establish a territory was for a MTFG to move to another site. When such family groups in marginal and secondary habitat made frequent movements during the winter-dry months to water and feed outside their home ranges, they occasionally came upon unoccupied and better sites than their own. If allowed to stay without excessive interference from neighboring territorial males, they began to return daily until the new location became the group's new feeding territory. If the new location was poor habitat itself, the MTFG discontinued returning within a few weeks. However, several MTFGs became PTFGs by transferring to new and better sites. When territory 207 was abandoned in June 1970, it was first regarded as a neutral zone by outside groups. In the afternoon of 7 July 1970 nine MTFGs and one SM fed tranquilly side by side where group 207 had formerly been. Eventually, after two months of competition for the site, two MTFGs (231 and 232) became permanently established there. Nine MTFGs reestablished themselves on a new territory during March (1), June (3), July (1) and August (4), when water and forage began to be scarce.

The third but less common way in which territories were established was by Mobile Family Groups. Males first obtained family members and then a territorial site instead of the other way around as done by most Solo Males. There was no sure way to differentiate between a MTFG and a MFG unless the MTFG was known and regularly used the study area. However, a MFG could generally be distinguished from MTFGs by its greater mobility, greater readiness to flee from attacking territorial males and smaller group size; a MFG commonly included only old-juvenile and young-yearling females, or an adult female and her cria with the adult male.

MFGs were formed when non-territorial SMs or adult males from MGs secured wandering and unattached females. Observations were made of MGs chasing and attempting to pick up adult female-cria pairs and young-yearlings without groups. Larger and more aggressive males were often more active in their pursuit and even "protective" of the female from other smaller and more playful males. A complete sequence involving the same individuals was not seen, but the larger and more zealous males were believed to separate themselves from the MG with their newly captured partners to become MFGs. A MFG was observed returning to a MG of 40 animals for two hours before moving on again and a male was seen trying to force a yearling female into a MG.

Four MFGs became established as territorial family groups in the study area, one each in the months of December, January, February and March. In three cases the male was accompanied by an adult female and her cria; the fourth male was accompanied by five near-yearling females.

Those MFGs with only old-juvenile or young-yearling females were short lived. From observations of MFGs moving through the study area, it appeared that the young females did not remain with such highly mobile groups, but left to join SMs with established territories or family groups with territories in which they were allowed to stay.

Family group formation

After a SM had an established territory, he then attempted to obtain females for his family group. This took an average of 6 months among the seven SMs followed closely. One male was by himself for only 1 month, yet two others were alone for 12 months. One of the latter males had a yearling female in his territory for only 3 weeks before she disappeared, and another 4 months passed before a female-cria pair joined him.

Even when without females, SMs vigorously defended their territories against trespassing male and family groups and actively defended their boundaries with neighbors. A SM returned daily from his sleeping area to pass the entire day by himself within his territory.

Territorial SMs without family groups were observed to occasionally spend time with MGs. For example, on 2 July 1970 SM 229 left his territory to chase a MG of 27 animals 700 m away; he then grazed with them before returning to his territory. SM 229 once joined 13 males and passed the entire afternoon with them grazing some 900 m away from his territory. On 22 September 1970 SM 105 passed the morning and part of the afternoon with three adult males in his territory. In late February 1971 the same SM allowed six yearling males to enter his territory; the male wandered with them some 900 m beyond his territory before returning.

A solo territorial male acquired his females from MTFGs moving through the area, yearling females without family groups, or an occasional unattached adult female with or without a cria. SMs frequently took on yearling females. For example, in June 1971 six out of the nine females recently recruited by males forming family groups were yearlings.

When a SM tried to take a female from a group, the female's male vigorously defended her and the two males often engaged in long hard chases and fighting. In only five out of 20 attempts were females forcefully removed from their family groups by a SM. Females could thus be obtained from family groups by SMs, but few attempts were made, probably because of the high energy costs.

Several times a territorial SM chased and forced a newly recruited yearling female back to his territory after an absence of several hours. Territorial SMs would sometimes suddenly leave their territory in early morning and run directly from the observation area for no apparent reason, only to return in the afternoon. I suspect they were looking for females during these forays.

A territorial SM rarely attempted to take away an adult female from a neighboring family group. The obvious disadvantages of doing so were the presence and harrassment of the other male attempting to retrieve his former mate and the female's attempts to return to her former group. In one such case, SM 208 successfully separated and held onto an unwilling adult female and cria from his neighbor 207, but only after much fighting and chasing between the two males for 2 days.

Once a SM obtained group members, he discontinued forays from his territory, but might still attempt to force a female away from an outside group passing through the area. He also turned his attention toward keeping the new members in his territory and was temporarily less occupied with border defense. New members might, at first, wander from or leave the territory, but the male promptly forced them back.

Family group cohesion and stability

Changes in size and composition of family groups were largely due to births and subsequent expulsion of crias. Adult females rarely shifted from one territorial male to another as occurs with a number of other ungulates. With a few exceptions, the same adult females remained in family group 211 throughout the study. One new female did join the group 15 months after I started observing it; one female died 5 months later; and several females joined the group after

23 months. In most groups, when there was a change in the number of adult females, it involved only one or two individuals. Group 207 was an exception because the adult male allowed females to enter and leave at will.

Some females temporarily left their family groups during the birth season to look for lost or separated crias, and others sometimes left with their very young crias and moved to higher terrain in the direction of the sleeping grounds. Females were obviously nervous with their new crias during the first 1 to 2 weeks after birth and would retreat at even the slightest sign of potential disturbance or danger. The source of disturbance might have stemmed from human activity in the area, but often the cause of female uneasiness was not apparent. If the pair left and the group failed to follow or the male didn't force them to remain, they were away only for a few hours. Uncommonly an adult female would be absent from her home group for several days during the birth season, only to return with or without her cria.

Vicuna entering family groups

Prevented from entering. Territorial males did not always accept outside females and young vicuna attempting to enter their groups. During some 3,300 hours of observation over 2 years family group males were observed 138 times out of 240 occurrences to prevent the entry of non-members into their groups. In half of these he rejected an adult female with her cria ($P<.005$), 22 percent were adult females by themselves, 15 percent were single crias in search of a group to join and the 12 percent balance were yearlings. Although the highest rejection rate of females with crias was in November, December and January (Figure 43), there was no significant difference between seasons, i.e., the proportion of rejection compared to acceptance was high year-round. The rejection rate of outsiders attempting to enter family groups for the four seasons beginning in the fall was 2.2, 4.6, 6.3 and 4.0 per 100 hours of observation.

In the late dry season and the months before the birth season, groups became increasingly more closed to outsiders. Adult females with crias were especially unwelcome and were driven away by the resident territorial male. For example, on 16 September 1969 a female with cria repeatedly attempted to enter family groups, but was always driven off by the male of the group she was trying to enter. In another case in late January 1971, a female cria having been expelled from her own group was rejected from four other groups she tried to enter.

Although it was the territorial male that chased away outsiders, two unusual observations were made in which the adult females of the family group prevented outsiders from entering and staying with their group. One case involved the rejection of a yearling female and the other an adult female and her cria. Koford (1957) reported it was female vicunas that chased outside females trying to enter family groups, and not the male, as regularly seen during this study. There was no apparent reason for the difference between Koford's observations and mine.

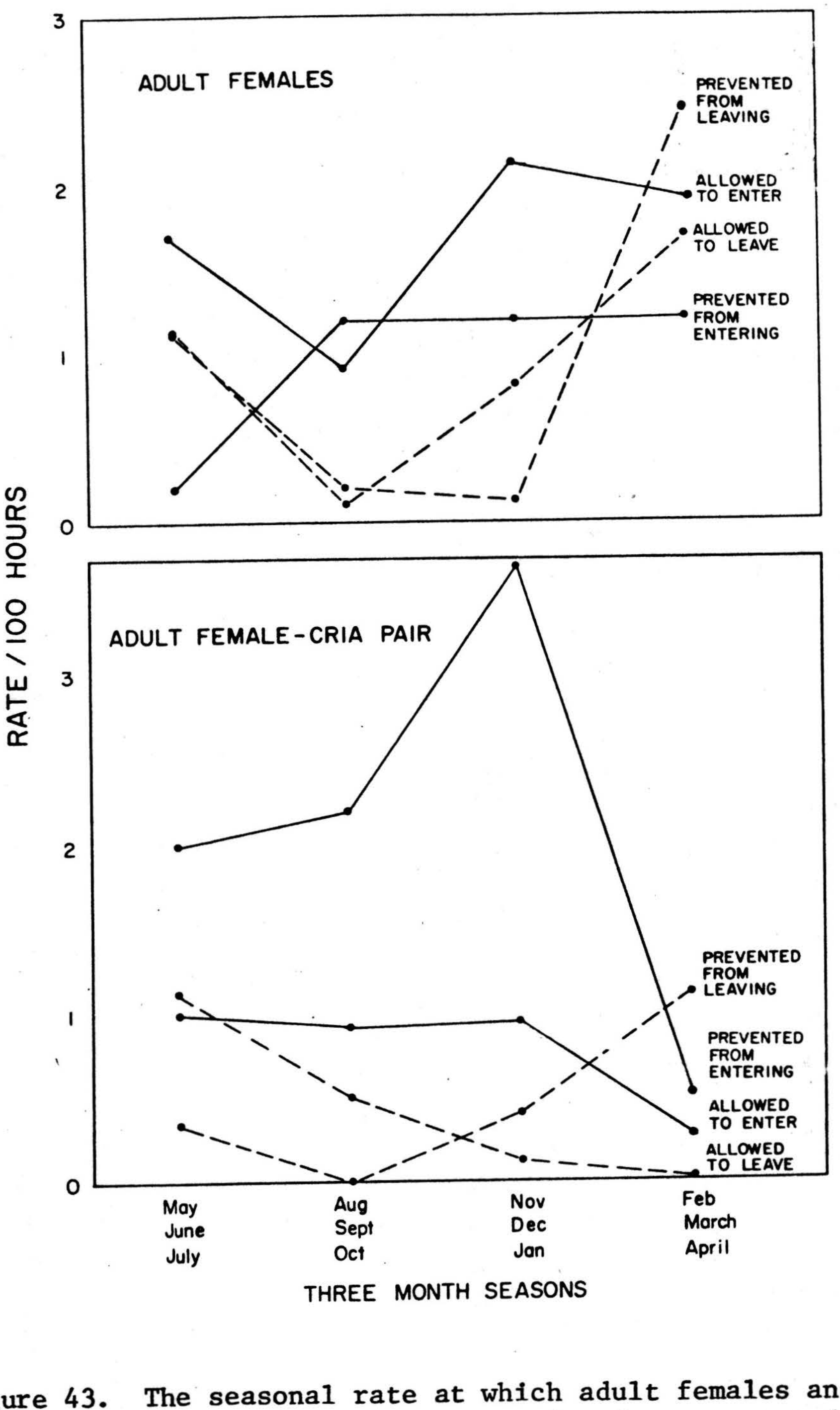

Figure 43. The seasonal rate at which adult females and adult female-cria pairs were allowed or prevented from entering or leaving family groups. Total observations of adult females was 139 and of female-cria pairs was 126.

Allowed to enter. Out of 240 attempts to enter a group there were 102 instances of animals entering without interference. Of these 78 percent temporarily entered the group for a few minutes to several hours before leaving and only 23 percent (six adult females, three females with crias and two yearlings) permanently entered and remained with the group. Acceptance into a group was determined by whether or not the male chased the animal away or permitted it to stay. An undetermined number of those individuals that only temporarily joined the group left because of threats from the male.

Half of those that entered groups without initial interference were adult females ($P < .01$), 26 percent adult females with their crias, 15 percent yearlings and 9 percent crias. Sixty-three percent of the attempts by adult females to enter a group were successful, in contrast only 28 percent of attempts by adult females with crias and 32 percent by single crias were successful ($P < .01$). Females had least chance of entering a group in winter ($P < .05$), a season when forage was most critical.

During January through March an aggressive yearling or an adult female sometimes trotted from one family group to the next seeking entry. The behavior was completely atypical for females established within a group, except when defending a male cria against an attacking family group adult male. Acting aggressive involved a high body posture, neck straight up, ears forward, the tail in an aggressive position of vertical or an upward arch and trotting about with quick stops and starts. The intruder acted aggressively when she approached the group and when the resident male came toward her. Some aggressively acting females during April and May were yearling females in estrus without an established family group.

On two occasions when a wandering yearling female approached a family group, the territorial male displayed an unusual behavior. After having walked out from his group to meet the approaching yearling female, the male turned his back to her and took several short steps in the direction of his group with his knees slightly bent and neck partially curled posteriorly over his back. In one instance the yearling did not stop but trotted past the group. In the second instance the yearling remained and grazed near the group for an hour. The next day a yearling female had permanently joined the same group. Perhaps the male's initial behavior was an appeasement or acceptance posture indicating no aggression to the outsider seeking entry into the group.

Vicuna leaving family groups

Prevented from leaving. Animals were prevented from leaving their family groups 49 times out of 105 attempts. These involved adult females (59 percent), females with crias (27 percent) and yearlings and crias (14 percent). It was especially high in summer when adult males prevented flighty new mothers and females who lost their crias and new group members from leaving. Sometimes the male forced a female back to his group after she became separated while the group was chased by a territorial male. At other times he retrieved a female visiting a neighboring group while looking for her cria; chased back a yearling female who had followed him while he was defending a territory boundary; or retrieved one of his group's crias that had been visiting a neighboring group.

Allowed to leave. Vicuna left their family groups without interference from the resident male in 56 out of 105 attempts. It was highest when persistent females left the family group to search for missing crias. No males were seen to allow females with crias to leave the family group and territory in summer.

Temporary transfer of crias between family groups

An exception to the highly closed vicuna social group was the permitting of crias temporarily to join neighboring family units. Almost all territorial males were tolerant of visiting crias from a neighboring group, but some regularly evicted any non-member cria attempting to enter his group. Crias began visiting neighboring groups when 1 to 2 months old. They went by themselves or with one or two other siblings. Visiting crias sought crias in other groups, where they spent most of their time chasing with some biting, neck wrestling and mock mounting. Such play activities were possibly an important socialization mechanism for vicuna crias.

Visiting crias remained with another group from a few minutes to several hours and even occasionally overnight. The rate at which crias made such visits to neighboring groups increased steadily from April (1.2/100 hours) to a peak in August (6.0/100 hours), then sharply decreased in September (1.4/100 hours) when groups became increasingly closed to outsiders.

While crias were playing with crias in a neighboring group, their mothers often became nervous about their absent offspring. A mother would regularly look up from grazing in the direction of her cria. Mothers and adult males might leave their territory to retrieve missing crias from neighboring groups. Once the male had to force the visiting cria and searching mother back to the home territory.

While other males were becoming more intolerant of outside crias visiting their groups in the late dry season, territorial SMs permissively allowed neighboring crias to join them. These same SMs would take on near-yearling and young-yearling females as their first family group members in the following months.

Family group longevity

The vicuna PTFG was a permanent year-round entity. Family groups disbanded and dissolved only when the resident male died or a marauding SM broke up the group.

Ten out of 37 groups (27 percent) were present 28 months of the study. Eight groups (22 percent) were present at the beginning, but disbanded during the study ($\overline{x}$ = 20 months, 9-27). An additional 13 groups (35 percent) became established and were still present at the end of the investigation ($\overline{x}$ = 13 months, 3-23). Only six groups (16 percent) formed and disbanded during the 28-month period, the mean longevity of these being 10 months (2-16). A greater number of MTFGs (12) became established than PTFGs (5), indicating that preferred and favorable habitat was already near saturation and most of the expanding population became established in marginal and secondary habitat.

Aggressive Behavior Within the Family Group

Ear and head positions, body orientation and body movements were important elements of agonistic behavior between interacting vicuna. Dominance was recognized by biting, kicking, chasing and more subtle behaviors such as ear position. An animal was considered subordinate if it avoided the other by retreating or turning away during an encounter. The most common avoidance behavior was turning the head and even swinging the long neck away from the threatening animal (Head Turn Away). Other avoidance behaviors included Dropping Head to feed, Turning Body away from aggressor, Standing Motionless, Moving Away and the Submissive Crouch. The recipient also dropped its ears in response to a threat, but the dominant animal usually dropped its ears to a lower level than the recipient. Thus the individual with lower ear position was invariably the dominant individual of an interacting pair.

In the Submissive Crouch the animal walked or stood in a crouched position with the knees bent, head tucked in, ears horizontal, neck arched posteriorly over the back and the tail in a full forward curl (Figure 44). Crias commonly assumed the Submissive Crouch when threatened or attacked by the family group's adult male and in some cases when an adult female threatened her own female cria.

Figure 44. Submissive Crouch by a near-yearling vicuna cria.

Several forms of this crouching behavior were observed: Nursing-, Semi-, Full- (described above), Exaggerated- and Forced-Submissive Crouches. The Nursing-Submissive Crouch was the posture taken by crias when approaching and supplicating to nurse from their mothers. It was believed to be the origin of the other forms of Submissive Crouches. In the Exaggerated Submissive Crouch, the head nearly touched the back and the knees almost or actually touched the ground. The frequency of this posture increased before the crias' expulsion from the family group by the adult male. Presumably the crouch could delay the time of expulsion of the cria from the family group by appeasing the adult male.

Intragroup social hierarchy

To better understand the relationships between animals within a group, observations were concentrated on one group. Over a six month period from August 1970 to January 1971, aggression among members of family group 211 was intensively studied. The eight members present at the beginning of this period were the Adult Male; four adult females, One Eye, Large Dark, Large Light and Two Dent; and three crias, Tagged Female Cria, Machito and Hembrita. The mother-cria relationships were as follows: One Eye and Tagged Female Cria, Large Dark and Machito, Large Light and Hembrita. The Tagged Female Cria was the oldest cria (born 6 March), followed by Machito (8 March) and Hembrita (16 March).

An average of 16 encounters per hour was observed within group 211. The group's activity had a profound effect upon the rate of aggression. Aggression was lowest when animals were intensively feeding and individuals only occasionally moved to their next feeding spot. Aggression between animals increased nearly 20-fold when the group simultaneously fed and walked and 40-fold when walking as a group (Table 12). The increased probability of animals approaching each other more closely, violating individual distances and animals trying to pass one another caused the rate to increase for a moving group. Only 5 percent of all intragroup encounters (n = 651) involved chasing, kicking or biting. The remainder were more subtle involving ear and body postures.

A stable, straight line social hierarchy existed within the vicuna family group 211, with the male dominant over all group members and the adult females dominant over the crias (Table 13). The adult female One Eye was only present during the first part of the study period before her death. Thereafter, Large Dark was the new dominant female. The dominant Adult Male and the top ranking female received the least amount of aggression in the group. The male was most aggressive towards the lowest ranking female and crias, while the bottom ranking adult female restricted her threats almost entirely to the crias (Table 13).

Older crias in group 211 were dominant over younger ones, even though the dominant Tagged Female Cria was only two days older and eventually smaller than the male cria, Machito. Crias' social rank was also the same as their mothers, i.e., the highest ranking female had the highest ranking cria and the second ranking female with second ranking cria; the lowest ranking adult female Two Dent did not

Table 12. Rates of aggression between animals in group 211 as related to their activity.

Activity	Number Of Encounters	Hours Sampled	Encounters Per Hour	Total Number Of Animals Present	Encounters Per Animal Per Hour
Intensively Feeding	245	32.2	7.6	723	0.011
Feeding and Walking	206	6.3	32.7	160	0.204
Walking	254	4.6	55.8	132	0.423
TOTAL	705	43.0	16.4	1015	0.016

Table 13. Rates of aggression (encounters/10 hours) between paired members of group 211. Boxed numbers are mother to offspring encounters. N = 543 encounters. September 1970 to January 1971.

	Individual	Hours Present	Subordinate								Total Dominant	Percent of Encounters Dominant
			Male	One Eye	Large Dark	Large Light	Two Dent	Tagged ♀ Cria	Machito	Hembrita		
Dominant	Male	35.6	-	0	1.1	0.6	2.3	5.3	4.2	11.5	25.0	96%
	One Eye	10.2	0	-	6.9	2.0	5.9	$\boxed{4.9}$	2.0	3.9	25.6	81%
	Large Dark	35.6	0.3	3.0	-	8.7	30.1	8.7	$\boxed{6.7}$	10.1	67.6	92%
	Large Light	35.6	0.6	2.9	1.1	-	10.7	9.3	5.5	$\boxed{9.6}$	39.7	72%
	Two Dent	35.6	0	0	0.8	1.7	-	9.9	5.8	6.2	24.4	28%
	Tagged ♀ Cria	17.2	0.6	0	0	0.6	2.9	-	14.6	6.9	25.6	39%
	Machito	23.9	0	0	0	0.4	0.4	2.9	-	4.2	7.9	18%
	Hembrita	35.6	0	0	0	0	0	1.2	3.0	-	4.2	5%
	Total Subordinate		1.5	5.9	9.9	14.0	52.3	42.2	41.8	52.4	-	-

have a cria. At 7 to 8 months of age the dominant cria began to show aggressive behavior towards the least dominant adult female.

Consequences of intragroup social hierarchy

Dominant animals commonly displaced subordinate individuals from their grazing sites when the group was feeding. During the dry season when drinking from small springs only a few meters in size, members were forced close to each other. The frequency of aggressive encounters was high, with dominant animals forcing subordinate ones to wait or move to another drinking spot. Although all animals eventually had an opportunity to drink, dominant animals had first access.

When the group moved from the sleeping to feeding territory they walked in order of rank: adult male, females and crias. One Eye was commonly the lead female before her death. Afterwards, Large Light usually followed the male and not the new dominant Large Dark as might be expected.

The male regularly (14 of 15 observations) initiated and led the group each morning from the sleeping territory to its feeding territory. He walked 20 to 50 m in front of the group. So strong was this leadership-follower relationship between the male and his females that whenever he moved off the line of travel to defend his territory the group would wait until he returned before resuming their movement. Thus on 5 November 1970 the male initiated the group's movement toward the feeding territory three times, but was interrupted twice when he left to defend his sleeping territory. The group waited for the absent male, feeding in place until he returned and resumed leading them to the feeding territory.

In contrast to the above leadership role of the male when moving between the sleeping and feeding territory, the male did not lead the group when it left its feeding territory during the dry season for a few hours to drink from the river or spring in a neutral zone. Instead, the dominant female One Eye initiated the movement and led the group from the feeding territory (6 of 7 observations). The move started when the male was at the opposite side of the territory involved in defense, suggesting the female was avoiding the possibility of the male preventing their departure. Once outside the feeding territory she did not necessarily remain the lead animal, but was replaced by other adult females. The male was usually last in line. The group ceased leaving its feeding territory to water after One Eye died. The one time it did leave, the group hesitatingly followed the male's initiation and lead. The male led the group when returning to the feeding territory from a neutral zone.

Probably the most important consequence of intragroup aggression and the associated social ranking of group members, was the forceful expulsion of the juvenile members from the group. Young males were forced out when 4 to 9 months old and young females when 10 to 11 months old. In July and August when male crias were first beginning to be expelled from groups, water and food were becoming progressively more limited and all crias were being weaned. Because females were still attached to their male crias, they vigorously defended their offspring against the adult male. The first few times a male cria was attacked and chased from the territory, it rejoined the group by the end of the day.

The female's protection of her cria waned as the young male became older and was fully weaned. But persistent attacks on the male cria by the adult male while the female-cria bond was still strong caused some females to leave with their crias. If she left in spite of the male's attempts to stop her, he invariably forced the female back to the group with the cria still at her side. Rigorous chases across the pampa were seen during this period when territorial males attempted to force a separated female and male cria, or sometimes just the female, back to their groups. The female's defense of her male cria and her unwillingness to remain with the group without her unweaned cria, prolonged the cria's membership with the family group. It also acted as a check against early separation of mother and offspring. Only after a number of expulsion attempts over a period of several weeks was the male cria finally and permanently displaced from the group.

With the expulsion of the male cria and the disappearance of Tagged Female Cria soon after her mother's death, only the young Hembrita remained in group 211 during January. She was frequently threatened by the other group members (8.0 encounters/hour). The level of antagonism directed to the female cria from the Adult Male increased markedly during her final weeks with the group (Figure 45). The female's high level of antagonism towards her own cria was a decisive factor too. Instead of protection, as females had shown for their male

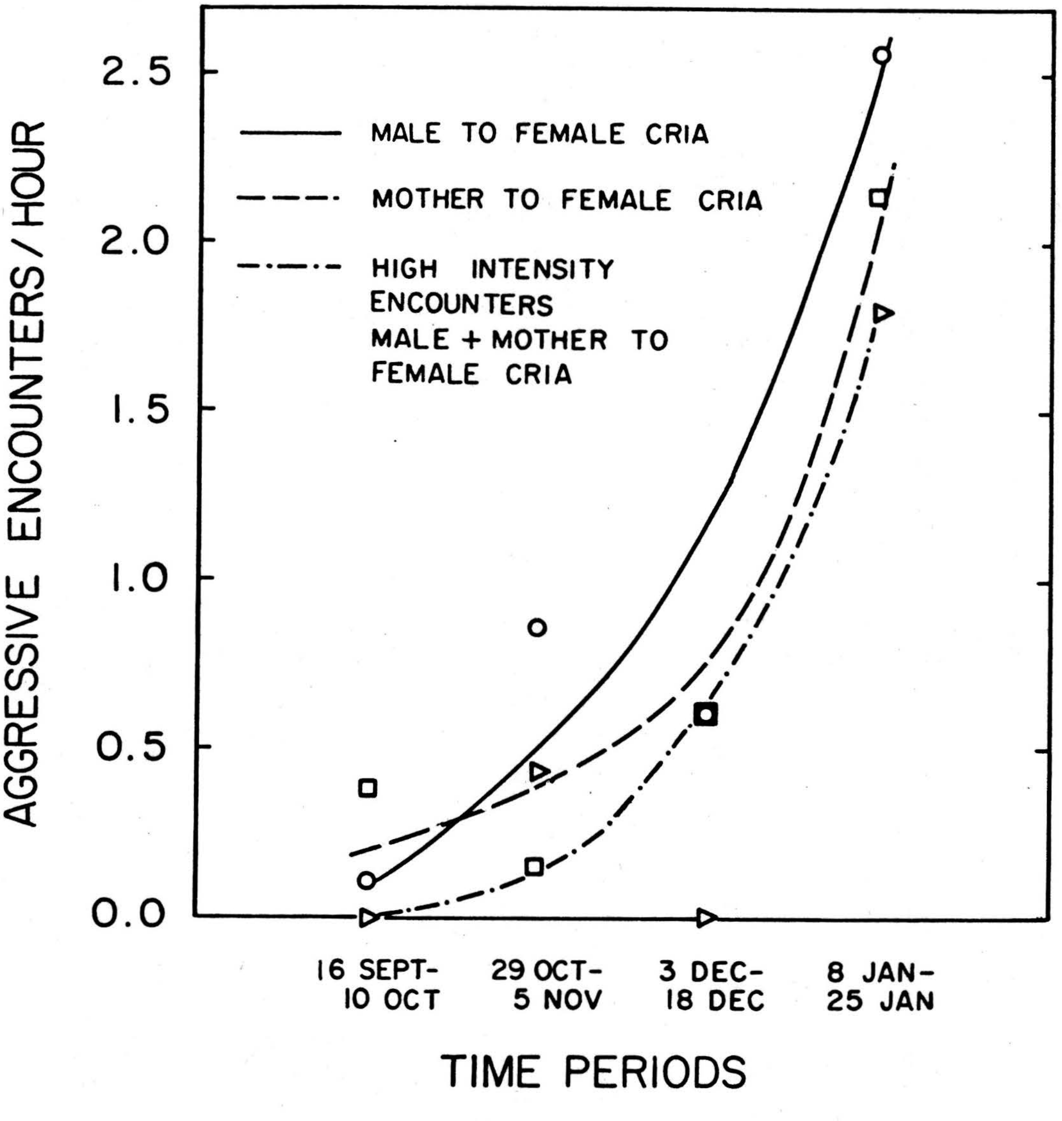

Figure 45. Rate of aggression from adult male and mother to female cria leading up to her expulsion.

crias under attack by the family group male, the mother of the female cria contributed to that aggression (Figure 45). The aggression of the other two adult females in group 211 to the female cria was almost as high as the mother's, increasing from 0.1 to 1.6 encounter/hour/female over the last three months the cria was with the group.

The frequency of Submissive Crouches by Hembrita paralleled the increasing aggression she received. In early November, 3 months before her expulsion, she first began making Submissive Crouches in response to threats from the male. Submissive Crouches were also caused by aggression from her mother 1 month before her expulsion. Eighty percent of Submissive Crouches by Hembrita were during the final 2 weeks with the group. Forced-Submissive Crouches were especially common during this period. In this form of crouch the female cria might suddenly and unexpectedly approach the male in a Submissive Crouch resulting in his first threatening her, then typically avoiding her by turning or walking away. Forced-Submissive Crouches occurred especially in the early morning. Though there were no quantitative measurements made, the behavior appears to inhibit the male's aggression toward the cria. If so, then the behavior would be adaptive in delaying her expulsion and prolonging her stay with the family group.

Of 63 Submissive Crouches made by Hembrita during her last three months in group 211, 67 percent were in response to the Adult Male, 18 percent to her mother, 5 percent to the dominant female and only 1 percent to the lowest ranking adult female. Submissive Crouches were related to the chances of being threatened by group members. Thus of

123 aggressive threats the Hembrita received, 36 percent were from the Adult Male, 25 percent from her mother, 22 percent from the dominant female and 17 percent from the lowest ranking female. This was illustrated on 8 January when the group was watering at the spring on the border of their territory. Although Hembrita was receiving high intensity threats from her mother causing her to go into Submissive Crouches, she was more concerned about the male. She constantly looked at the male, watching his movements and walked as closely as possible to her threatening mother.

On 25 January Hembrita was violently attacked and chased from the group by the Adult Male. During the morning from 0530 to 1055 the cria had gone into three Forced-Submissive Crouches with the male and received three high intensity threats per hour from her mother. Her expulsion was complete and final and she was not seen with the group again.

Twenty-one cases were observed of males expelling crias from family groups. In mid-February 1969 several adult females in group 207 were observed expelling a near-yearling female. It appeared the male had not fully expelled the female cria from his group and she was being driven out by adult females who would soon give birth.

Dispersal of subordinate individuals from a population has often been suggested as a consequence of agonistic behavior, but it has been only infrequently demonstrated in field studies (see Watson and Moss, 1970; King, 1973; Barash, 1974). For the vicuna aggressive behavior from territorial males caused the dispersal of the lowest ranking and youngest individuals (male and female crias) from family groups. Dispersal of young female vicunas reduced the number of feeding and reproducing individuals within feeding territories.

During November through January in group 211 the lowest ranking adult female Two Dent received four times as many threats as the next ranking adult female. Because of the frequency and intensity of the aggression, I expected her to be forced from the group or to leave on her own accord. This high level of aggression to the lowest-ranking female suggests that another possible consequence of intragroup aggression might be the expulsion of such lowest ranking adult females by the adult male or the female's voluntary departure from the group.

Defecation-Urination and Territorial Marking

The vicuna is one of the few hoofed animals that always uses traditional dung piles, a behavior that has profound environmental and social consequences for the species.

Animals in all vicuna social groups eliminated on dung piles. Members of family groups defecated and urinated on dung piles in their sleeping territory, feeding territory, between the two territories and in unoccupied zones of neutrality between their feeding territory and dry season watering sites. Even crias used dung piles from the time they first started eliminating. MGs used dung piles in neutral zones or even within a territory if they happened to be passing through one.

Description of defecation-urination behavior

All vicuna showed basically the same preliminary behaviors of smelling a dung pile, forefeet kneading, turning and positioning before defecating or urinating. Pilters (1956) observed the same behaviors in captive vicuna. There were two distinct types of defecation-urination: Defecation-Urination (DUs) done by all animals primarily as routine elimination, and Defecation-Urination-Displays (DUDs) which were special forms of DUs performed by territorial adult males during the defense of territories.

The first step in DU was smelling, occurring 93 percent of the time (Table 14). The adult male smelled slightly more regularly in DU than did others ($P < .20$). Next came kneading of the dung pile with the forefeet while standing in place. This occurred about a quarter of the time. Crias kneaded the most (39 percent, $n = 104$), adult females intermediate (27 percent, $n = 169$), and the adult male the least (18 percent, $n = 56$). Kneading may have been a means of spreading individual or group scent throughout the territory.

Following kneading came turning. Adult females and crias turned about half the time, primarily with a one-quarter turn. The adult male turned slightly more frequently than other group members ($P < .20$).

A common DU sequence for adult females and crias was to walk up to and top immediately over a dung pile, lower the head to smell the site, make a turn, position the body with the hindquarters lowered and defecate or urinate. This smell-turn-position-defecate-urinate sequence was observed 27 percent of the time for adult females and

Table 14. Preliminary behaviors connected with Defecation-Urination (DU) and Defecation-Urination Displays (DUD) in family group 211.

	Percent Occurrence					
	DU				DUD	
	Adult Females And Crias		Adult Male (No Obvious Territorial Defense)		Adult Male (During Territorial Defense)	
N =	392		64		84	
Smelled	92		97		96	
Kneaded	28		20		4	
Turn 1/4	41	49	39	58	42	83
1/2	7		17		36	
3/4	1		2		5	
Head Shake	2		6		4	
Flehmen	1		13		6	

crias (n = 407) and 42 percent for the adult male (n = 64). The closely related smell-position-DU sequence without turning was equally common for females and crias (28 percent), but less for the male (14 percent) in group 211.

Once in position to eliminate, vicuna defecated 60 percent of the time, urinated only 5 percent, defecated and urinated 19 percent and positioned without eliminating 16 percent (n = 561). In the feeding territory, females positioned without eliminating 1 percent of the time (n = 150) and crias 4 percent (n = 95). There was a marked increased in the frequency of animals going through the preliminary DU behavioral sequence without eliminating when preparing to leave the feeding territory: 33 percent of the time by females (n = 24) and 64 percent by crias (n = 14). Once the group was outside the territory and moving through neutral zones, females positioned without defecating or urinating 83 percent of the time (n = 24) and crias 100 percent (n = 16).

The form of DUD was similar to the DU (Table 14). It always occurred, however, during the defense of a territory and the behavior itself differed from DU in that the male kneaded less ($P < .01$), turned more often, turned further than a quarter turn ($P < .01$) and went through the preliminary DU behaviors more often without eliminating (39 percent vs. 15 percent, n = 79 and 64; $P < .01$). Male 211 stopped at a dung pile during 58 percent (n = 196) of all intergroup encounters for a DUD: 47 percent were the smell-turn-position-DU sequence and 27 percent the smell-turn-position without eliminating.

Male 211 DUDed primarily (92 percent, n = 102) when defending his territory against trespassers. The other eight percent occurred when the male had trespassed onto a neighbors territory; he was then chased out and retreated into his own territory where he DUDed. Most DUDs occurred at the terminal point of an encounter (47 percent) or during the male's return toward his group (29 percent). Thus, DUDs tended to be performed towards the outer portion of the territory, but not necessarily on the border. Pilter (1956) also reported that captive male vicunas conspicuously defecated along their enclosing fence, behind which related animals were penned.

The male was laterally oriented to his opponent 56 percent of the time (n = 80). But for male 211 balance appeared to be more important since he almost always (90 percent, n = 39) faced uphill with his hindquarters downhill. During DUDs the male defecated 60 percent of the time (n = 87); he positioned without eliminating 39 percent, twice as frequent as in DUs.

During intensive or continuous territorial defense, the DUD position was often maintained for prolonged periods. For example, on 5 March 1970 when group 214 was being harassed and disrupted by SMs and MGs, the adjacent newly established territorial male 228 stood near the common border. Changing dung piles frequently, he positioned in a DUD over the same dung pile for as long as 28 minutes (DU positioning without eliminating lasted no more than 5 seconds). He appeared to be posting himself to keep marauding males from his area.

When two neighboring males were disputing a common boundary, they often approached within a few meters, stopped on dung piles within their own territory and performing a DUD. Sometimes they trotted from one dung pile to the next with their heads lowered to the ground, abruptly stopping over a dung pile, smelling, turning, and positioning without eliminating.

The frequency of DUDs was in relation to the potential threat or challenge that a social group offered to the defending territorial male. For example, 65 percent (n = 81) of encounters by male 211 with groups sharing a common border with him elicited this behavior, 60 percent (n = 15) when opposed to MGs, 52 percent (n = 25) with MTFGs moving through the area and only 33 percent (n = 15) with non-neighboring family groups.

Defecation-Urination Displays appeared to reinforce the male's possession of his territory through visual and scent marking behavior. The function of this behavior is hypothesized to be a display to the male's opponents and to assist the male in orientation to his own territorial boundaries. The display also prolongs territorial defense, perhaps affording the recipient additional time for retreat and reducing the defender's chances for a longer chase or even direct physical confrontation.

Context and rate of defecation-urination

The rate of Defecation-Urinations was greatly influenced by social context and site and was an indicator of individual anxiety in stressful situations. Changes in the group's location, activity and movement to or across the group's territorial borders caused a marked increase in the rate of DUs. Nearly all group members commonly used the same dung pile in succession when leaving the sleeping territory or feeding territory, or when moving between the feeding territory and a neutral zone.

Almost immediately after rising in the morning, each member walked to a nearby dung pile and defecated. Although not observed, I suspected animals also frequented the dung pile during the night. On one occasion group 211 passed the night slightly outside its sleeping territory and upon rising walked 50 m back into its sleeping territory before eliminating. During the day the DU rate was 2.5 times greater in the sleeping territory than in the feeding territory (Table 15).

As the group started to leave their sleeping territory, members filed up to a dung pile on the periphery of the territory and DUed at a rate 24 times higher than when in the feeding territory. While moving between their sleeping territory and feeding territory, an undefended corridor and part of their total home range, the DU rate was low and averaged only slightly more than the feeding territory rate.

Once within their feeding territory the mean DU rate was at its lowest and nearly equivalent for both adults and crias. The low DU rate possibly reflected the group's security within familiar and safe terrain. If the group moved to the territory's periphery, such as a spring or mutual boundary, the animals commonly defecated on their way. It appeared that the animals were orienting themselves or checking their location. For example, on 31 October 1970 when groups 211 and

Table 15. Defecation-Urination rate during daylight hours for all animals in group 211 and change in rate relative to feeding territory by age class and activity. August 1970 to January 1971.

Social Context	DU/Animal/Hour	Rate Relative to FT	
		Adults	Crias
Sleeping Territory	.033	2	4
Leaving Sleeping Territory	.315	22	28
Between Sleeping Territory and Feeding Territory	.017	1	2
Feeding Territory	.013	1	1
Leaving Feeding Territory	.646	46	54
Between Feeding Territory and Zone of Neutrality	.143	10	12
Zone of Neutrality	.423	28	40

208 came together at their mutual boundary, most members of both groups stopped and defecated just before coming to the border. The two groups then fed 5 to 10 m apart, separated by their common boundary. When the group was preparing to leave its feeding territory and cross the flat to water on the bottomland during the dry season, DUs were at their highest rate and 50 times more than when in the feeding territory.

Members frequently stopped at dung piles while moving through the narrow neutral corridor towards the neutral zone on the lower flat. The DUs were short, hurried and abbreviated forms of the usual complete DUs. Movement from the feeding territory to a neutral zone was direct and the animals walked fast. If the group strayed outside the neutral corridor and into adjacent territories, they were subject to attack from the territorial owners. I had the impression that the brief and truncated DUs were "checks" or confirmations of location. Since they regularly used the same route between their feeding territory and watering site during this time of year, it was quite possible animals were checking for previously used dung piles with their own or group odors, to insure they were within the safe neutral corridor.

While in the neutral zone animals DUed at the second highest rate compared to other social contexts; crias especially made frequent use of dung piles, most likely reconfirming their location and as a consequence of anxiety at being in unfamiliar terrain.

Crias and defecation-urination

Crias consistently showed a higher DU rate than adults in a variety of different social situations, especially when preparing to leave and when outside their territory (Table 15). Laboratory animals also have higher defecation rates under stressful situations (Bindra and Thompson, 1953). The crias' general level of anxiety was apparently higher as they prepared for and faced stressful situations out of their familiar home range.

There were two additional situations where a high rate of Defecation-Urinations among crias, both of which appeared stressful, also occurred. The first situation was when crias temporarily left their family group to associate with crias in a neighboring group. They frequently DUed as they left their area or arrived at the neighbor's territory. The second situation was during the final weeks before the female cria was ejected from the family group, a time when the adult male and females were frequently aggressive toward the cria. Thus the female cria, Hembrita, in group 211 showed a sharp increase in the frequency of defecation-urination in her final weeks before expulsion from the group (Figure 46).

Distribution, density and weight of dung piles

All dung piles within 128 ha of the study area were mapped, counted and weighed before the fall summer rains started in January 1971. Excrement had accumulated since the previous year's rainy season, so essentially one annual accumulation of fecal material was measured.

Distribution of dung piles on the slopes and flats coincided with

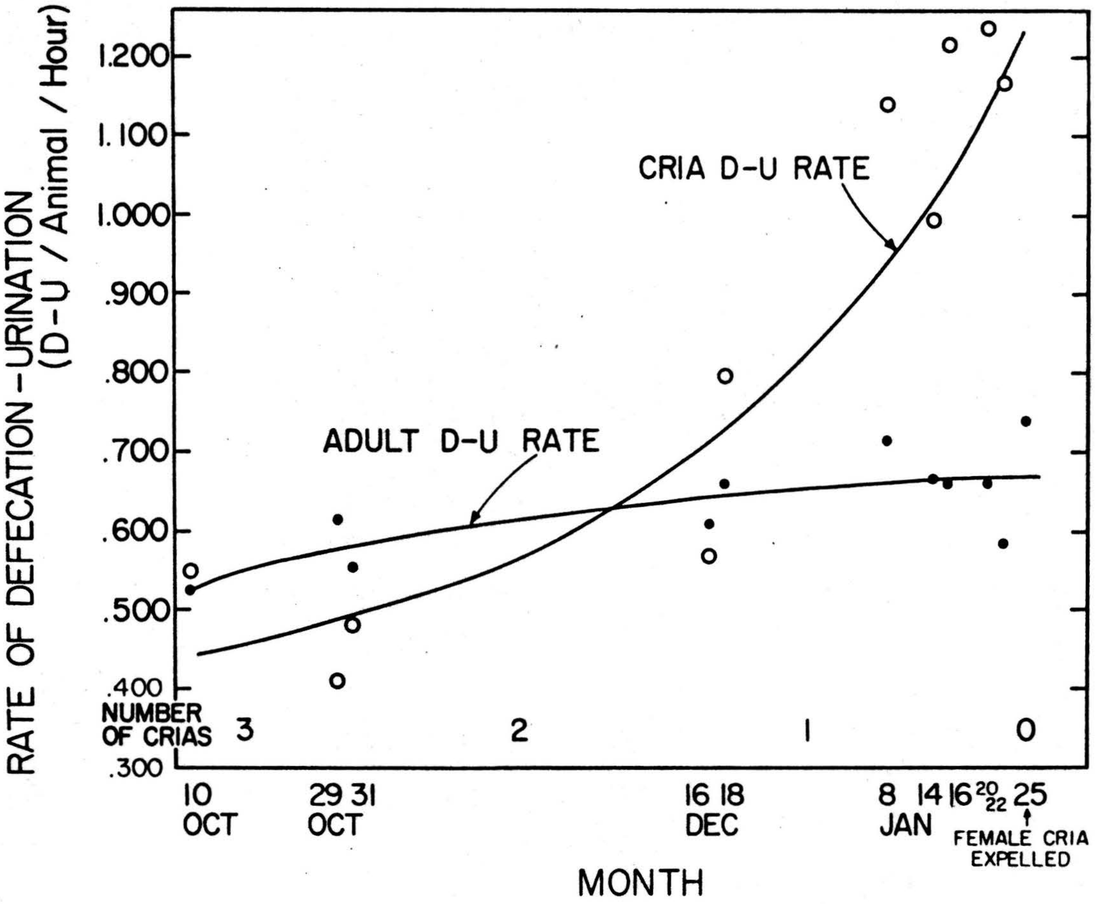

Figure 46. Comparison between adult and cria defecation-urination rate leading up to the female cria's expulsion from group 211. Adult n = 164, cria n = 78.

the downhill lines of excrement influenced vegetation and even tended to be in undulating rows on the level bottomland (Figure 47). Few dung piles were found within the coarse bunch grass community (VT-11) on the upper slope. Dung piles were found throughout the territory, and there was no indication that they were more common near boundaries, although lines of dung piles sometimes followed boundaries.

On the communal sleeping ground where family groups 208, 209, 211, 212, 219 and 227 had their sleeping territories, the density of dung piles was slightly higher (but not significantly) and their mean weights substantially greater ($P<.005$) than was found on the slope, flat and bottomland where feeding territories were located (Table 16). Total fecal material per unit area was over six times greater within sleeping territories than within feeding territories. This is what one would expect since vicuna were spending about as much time on sleeping territories as on feeding territories and were presumably moving about much less on the sleeping territory. Yet, the mean total amount of accumulated fecal material per average territory was greater in feeding territories than sleeping territories (Table 16), since the average feeding territory was seven times as large as the average sleeping territory.

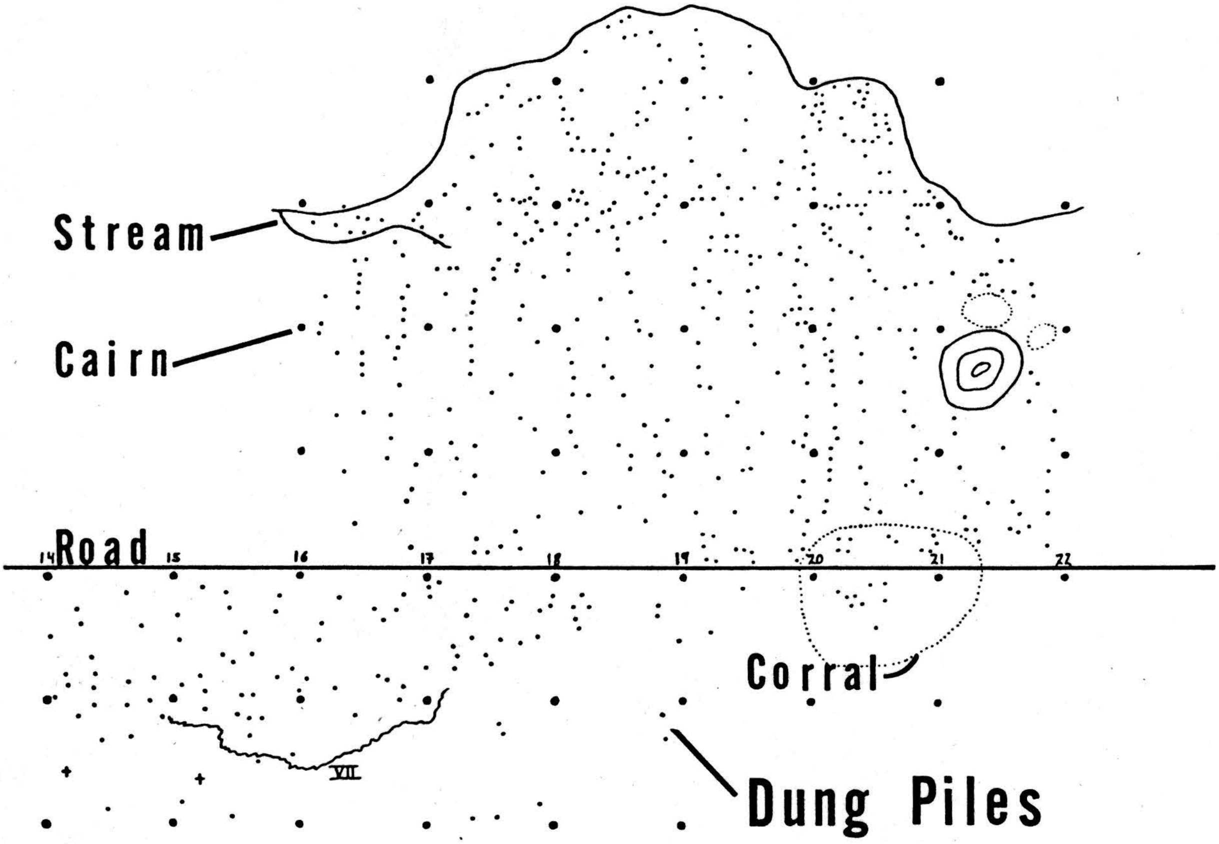

Figure 47. Distribution of dung piles on slope, flat and bottomland in portion of Zone I of Cupitay Valley study area.

Table 16. Density and dry matter weight of dung piles within a 150 ha portion of the study area. Weights represent one year's accumulation of fecal organic material.

Measurement	Sleeping Territories	Feeding Territories
Hectares Sampled	11.2	138.8
Dung Piles Present	75	588
Dung Piles/Ha	6.7	4.3
S.E.	1.48	0.43
Mean Dung Pile Weight In Kg	28.5	6.8
Range	2-80	2-56
S.E.	0.97	0.35
Mean Kg Of Fecal Material/Ha	191	29
Mean Kg Of Fecal Material Per Average Territory	497	534

DISCUSSION

Environment and Social Organization

Throughout its historic and present range the vicuna has been limited to the puna grasslands of the Andean altiplano. The vicuna is the only wild ungulate to prosper on this alpine grassland environment characterized by greatly fluctuating and freezing temperatures, light precipitation, short growing seasons and low plant production. Preferred and higher producing vegetation types for the vicuna were very limited in area and slowly renewing, but locally abundant in small and dispersed patches. At lower elevations the grassland gives way to brushland, habitat better suited to guanaco and huemul deer (Hippocamelus antisensis). Two conditions have favored sedentary habits of the vicuna: rainfall patterns are uniform over extensive areas of the altiplano and there is a sharp transition from grassland on the altiplano to brushland at lower elevations. Thus during the dry season vicuna do not have anywhere else they can go to find better sources of forage. These circumstances favor a territorial system.

A number of conditions must be met for a territorial system to be feasible. The resources for which animals compete must be defendable (Brown, 1964); they must be dependable and predictable in space and time (Wilson, 1975); and they must exist on small areas where plant community diversity and productivity fulfill the animal's living requirements (Geist, 1974). These are the conditions that exist in the altiplano: high visibility in this grassland allows the vicuna male to readily detect territorial interlopers; food is predictable in time and space even though there are marked seasonal changes in abundance of forage; food is locally abundant on patchy sites; and although visible natural landmarks for delineating territorial boundaries are limited, vicuna dung piles may in part substitute for this lack.

To establish a territory was a long and costly process for a male vicuna, involving many chases and fights. An average of 6 months elapsed before a male obtained females in his territory. Once the territory was established, the year-round need for food resources and the high cost of reestablishing a territory apparently made it more economical to defend the territory year-round. There were, however, peaks of territorial defense which coincided with seasons when competition for forage and estrus females was highest.

The size of social groups is considered to have evolved in response to two environmental factors: the distribution and density of essential resources and the level of predator pressure (Altmann, 1974). Animals of open grasslands rely upon early detection of approaching predators, concealment within a large group, and en masse defense or quick escape. Up to a point the larger the group size the more effectively the group can detect and cope with predators (Kummer, 1971; Treisman, 1975). But there will be selection for the group size that can most efficiently utilize the food supply. In the patchy but locally abundant vegetation of the altiplano, it would obviously be favorable to have small group sizes to reduce the time spent in travel to reach food. At night the detection of predators becomes more difficult, so one might expect larger group sizes to occur then. This is what occurs among baboons that spread out in small groups to feed during daytime, but reunite in larger groups for spending the night (Kummer, 1968). Perhaps it is for this reason that several vicuna family groups sleep close together in a compact cluster of sleeping territories. And for the same reason the 20 member all-male groups may receive this benefit in detection of predators where they sleep together in groups of this size. In daytime large male group size may also serve to detect and resist attacking territorial males.

When several vicuna family groups temporarily came together in small aggregations to drink in a neutral zone, this was believed due to the indefensibility of an essential resource with spatially restricted distribution. Altmann (1974) referred to resources that tend to be in a few places with concentrated abundance as "supermarkets." Some springs appeared to be such supermarkets to the vicuna, an obligate drinker. The few remaining sources of permanent water in the late dry season were under such heavy use by local and outside groups that they could not be defended by territorial males, even if the resource normally fell within their borders.

Mating System and Individual Fitness

Vicuna are polygamous like most mammals. In general, the greater the role of a male in rearing the young, the smaller degree of polygamy. Where the male serves only as sire and in no way aids in providing food or protection we find the highest degree of polygamy as in seals (Bartholomew, 1970). At the other extreme, amongst wolves, the male plays a vital role in providing food, in preparation of the den and in caring for the young. Here a system close to monogamy prevails. The vicuna falls in between. The male, through his strong territorial defense, is able to guarantee year-round supply of food. Depending upon his level of aggressiveness he may be able to provide food enough to support several females and their young.

The male vicuna has several strategies for enhancing his fitness. Fitness is defined as the contribution of one genotype to the next generation compared to other genotypes, natural selection eventually leading to the prevalence of genotypes with the highest fitness (Wilson, 1975). One assumes that selection has favored those individuals, both male and female, that can distinguish between the relative suitabilities of habitat and recognize those forage types with highest food value. Beyond this, the strongest males will be able to settle on these most suitable forage types and establish the largest possible territory commensurate with the degree of competition from rivals. These males will presumably be able to attract more females than those males forced either to establish smaller territories in this most suitable habitat, or to settle for a territory in less suitable habitat. Selection would favor those individual males that are able to determine at any instant which combination of habitat and degree of competition would result in maximum forage for the male and his future family group under these circumstances. These relationships have been discussed in detail for birds by Fretwell and Lucas (1969). At Pampa Galeras male vicuna that acquired the largest territories also acquired on the average the most forage, and in turn acquired the largest family group (Figure 48).

An additional strategy for the male vicuna is to forego attempts to acquire a territory until older and stronger. Such males tend to form all-male groups and made up 70 percent of all males during the study.

Once having gained his territory, the male's fitness will be further dependent upon the number of females he acquires, the more females the greater potential number of progeny. But production of young must depend closely upon the total forage within the male's territory. Therefore there will be some optimum number of females the male should acquire. The male should show increasing intolerance for additional females attempting to enter his territory and should reject those females that would actually reduce his overall fitness. It was, in fact, common for territorial males to be aggressive toward unattached females attempting to join family groups and to chase such outsiders away.

Having optimized his family group size, the male must also take steps to stabilize this size. Here natural selection must influence the amount of parental investment the male makes in his offspring (Trivers, 1972 and 1974). The male must be tolerant of his offspring up to the point where they have good chances of surviving on their own. At that point the male should evict the offspring. Territorial males did in fact expel their male and female crias. The male crias were

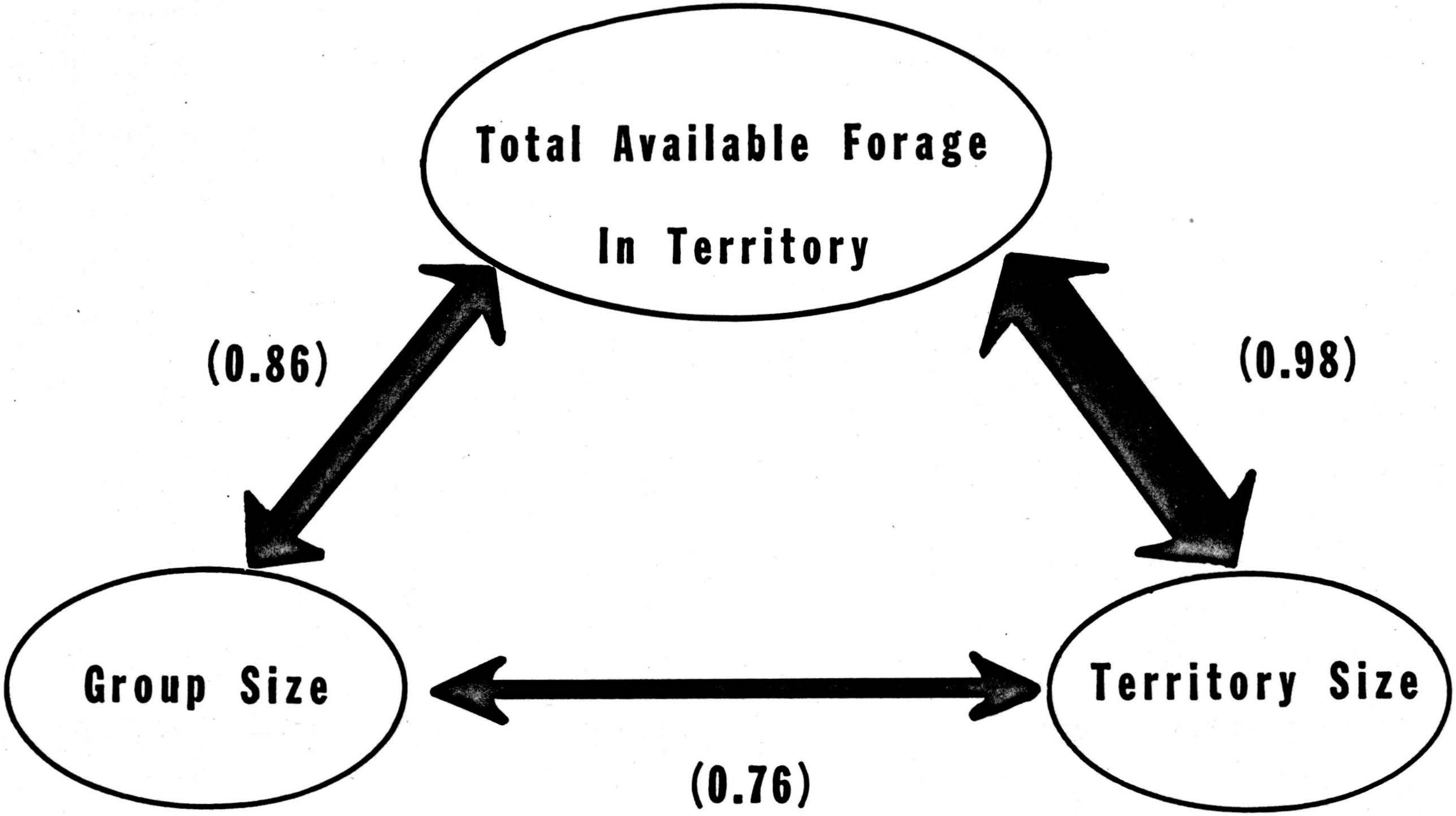

Figure 48. Correlations between forage production, group size and feeding territory size for 12 vicuna family groups in the spring of 1970. All significant at the .01 percent level.

expelled as much as several months before female crias. This may be because all surviving females participate in reproduction, while all males may not be able to establish a territory and reproduce. The female crias were permitted to remain in family groups until 4 to 8 weeks before the next birth season. Presumably the longer the female cria is allowed to remain and feed within the territory the greater her chance for survival becomes. Permanent retention of female crias would be good strategy in terms of the male's fitness since offspring of a cross between the adult male and his female crias would carry more of his genetic material than a cross between the adult male and the mother. But most females don't produce their first offspring until three years old, so the male would be carrying a nonproductive individual competing with productive females for limited forage. Unless the mother was nearing the age of declining productivity, it would be better for the male to expel his yearling female crias and retain the breeding adult females.

Strategies of adult females for maximizing their fitness differ from those of territorial males. The site and family group which a female selects may depend upon the characteristics of the environment (food and water abundance in relation to territory size and number of competing females and security from potential predation) or characteristics of the territorial male (size, rate of defense and whether the male accepts her).

In species where females meet the male only for breeding, such as the Uganda kob (Adenota kob Thomas;), elephant seal (Mirounga leonina) and sage grouse (Centrocercus urophasianus), the female must base her selection of males mostly on the behavior and physical characteristics of the male. In such a system selection should be for size, strength, degree of activity, experience and in general, sexual dimorphism in the male because of the strong competition between males for females. In contrast, with vicuna the females are permanently with males in year-round feeding territories, so they can base their selection much more on the actual resources of the site. In addition, the male's access to estrus females has already been determined long before the breeding season, so males do not directly compete for females at that time. The result is a minimum of time and energy spent on courtship and mating. All of these factors may account for the lack of sexual dimorphism in vicuna.

Female fitness also depends upon family group size. A female seeking the best place to settle might join a relatively inexperienced territorial Solo Male in the process of forming his family group and thus have few to no female members as competition; or she might select a long-established territorial male with a number of females. Yearling females most frequently joined Solo Males where there was least competition with other females, while adult females joined established family groups. Females must also balance the selection of a territory with good forage but more female competition, against territories with poorer forage but where the number of females might also be less.

A resident female's fitness declines with each additional female joining her family group. She would be expected then to be intolerant of intruding females seeking group membership, as was reported by Koford (1957), but rarely observed in this study.

Perhaps at the densities prevailing during this study it was better for the female to let the territorial male repel potential new females. In this way the resident females could devote more time to feeding and caring for their young. Such a family group system would tend to be more harmonious and be more effectively on guard against predators.

A consequence of the one-male territorial family social system in the vicuna was that it forced the bachelor males to take up residence in the less favorable parts of the habitat. They could survive there because they had lower energetic requirements than territorial males that were devoting additional energy into defense of the territory. This separate foraging of all-male groups from one-male family groups allowed better allocation of limited food resources to adult females that were usually pregnant or lactating as Kummer (1968 and 1971) found for the desert-dwelling hamadryas baboon (_Papio hamadryas_). Such separate foraging also occurs under poor conditions with all-male groups in the gelada baboon (_Theropithecus gelada_) that inhabits arid mountain and alpine environments of Ethiopia (Crook, 1966, 1970b).

Role of Territoriality in Regulation of Population Density

There are three prominent theories of the role of territoriality in regulating population density: (1) territoriality merely spreads out the population, but does not limit density (Lack, 1964); (2) territoriality operates so that with each additional territory it becomes more difficult for a newcomer to acquire a territory, but the system places no absolute limit on density (Elastic Disc theory of Huxley, 1934), and (3) territories have an upper limit to compressibility, and when a certain threshold is reached, newcomer males must then select territories in less favorable habitat (Buffer Mechanism theory of Kluyver and Tinbergen, 1953). A male vicuna in the process of establishing a territory should do whatever possible to maximize his fitness. He can select the best habitat and establish a territory as large as possible for his energies; select less favorable habitat but with the possibility of having a larger territory; or defer establishing a territory until he is stronger and more experienced.

What was the situation in Pampa Galeras during this investigation when the vicuna population was expanding? From 1968 to 1971 population density within the Reserve increased 36 percent (14 to 19 vicuna/km^2). At the beginning of the study, most vicuna in Cupitay Valley study area were in the best habitats. During the study, overall density increased slightly (16 percent, 19 to 22 vicuna/km^2), while family group density increased 45 percent (3.1 to 4.5 groups/km^2). The major part of this increase was in less favorable habitat. The increasing numbers of breeding age males brought increased competition for territories; the level of aggression between territorial males and the frequency of territorial defense increased.

Vicuna seemed to be operating under the Ideal Dominance Distribution system proposed by Fretwell and Lucas (1969), in which males do not have free choice of the habitat they select for a territory. The more vigorous males will acquire a somewhat better territory in terms of resources than those less vigorous. But as the population increases in density, there will be increased numbers of males seeking territories and a tendency for all territories to become less suitable as competition for space arises. In Brown's (1969a) classification, the population was at Density Level Two, in which the most attractive habitats were filled first. As competition rose, a male might do equally well by establishing a somewhat larger territory on marginal habitat as establishing a smaller territory on better habitat.

During the study group size of PTFGs declined substantially. Group size of MTFGs declined less, suggesting these territories had become relatively more favorable than in 1968 at the beginning of the study. Also the proportion of MTFGs increased and PTFGs decreased. By 1971, formerly unoccupied habitat in areas outside the study area and surrounding the Pampa Galeras Reserve had become populated with vicuna. Even poor habitats, such as the Tola shrub community, became occupied. Within the study area, at the end of each annual cycle and at the onset of the next birth season, family groups had been reduced to primary social units composed of an adult male and adult females. As a consequence, local density was relatively constant while the total surrounding population increased as the unoccupied habitats were filled. Although reproductive success was lower in Marginal Territorial Family Groups, territorial behavior maximized total population production by forcing the occupation of and reproduction in relatively poor habitats, as suggested by Brown (1969b) in his article on buffer effect of territoriality. The facts suggest that the population was responding rather like the Kluyver-Tinbergen model. The population had passed a saturation threshold and was spilling over into the lesser quality and unoccupied habitats.

Reproduction

Vicuna were strong seasonal breeders in spite of their close proximity to the equator. Ninety percent of all births occurred over a 6-week period when forage was optimum (most abundant) and nightly minimum temperatures stayed above freezing. Predictable seasonal production of forage has set and shortened the birth and mating season for the vicuna, a relationship also postulated for some ungulates by Geist (1974). Predictable daily afternoon storms appear to have further restricted births to the morning.

Females mated at the end of the growing season when they were in best physical condition. The unusually long 11-month gestation presumably permits slow fetal development over an extended period. This long gestation has perhaps evolved in response to year-round scarce food resources and the short annual growing season.

Vicuna Social Organization Compared to Other Ungulates

Most ungulate territorial systems studied to date are based upon mating and not feeding. Owen-Smith (1972) stated that territoriality in ungulates has evolved primarily as a system for ordering reproductive competition among males. If so, the vicuna's year-round territorial feeding system of permanent one-male groups is an exception.

Territoriality is common among African ungulates. Estes (1974) reported in his review of African bovid social organization that 85 percent of some 70 species of bovids were territorial during at least part of the year. In Jarman's (1974) skillful analysis and classification of African antelope social organization and ecology, Class C and especially Class D have similarities with the vicuna. Class D includes primarily three genera of the subfamily Alcelaphinae: Connochaetes (wildebeest), Damaliscus (tsessebe, topi, blesbok and bontebok) and Alcelaphus (Hartebeest). Antelopes of this subfamily lack sexual dimorphism. They have both migratory and non-migratory populations, or sedentary and nomadic phases within one population. In many areas there was a seasonal alternation between phases: the sedentary phase with its mosaic of breeding territories persisted while food was abundant, but changed to the nomadic phase of large mobile aggregations when food was restricted. Temporary mating territories could be established when moving herds remained stationary (Jarman, 1974).

The sedentary phase of Alcelaphinae social organization has many features in common with the vicuna: a proportion of adult males defends permanent year-round territories; territories are occupied by one-male and female-offspring groups (nursery herds); and non-territorial males form bachelor herds that may be driven into marginal habitat. An aspect that differs from the vicuna is that Alcelaphinae nursery herds moved within home ranges that overlap many male territories. It has been reported, however, under some conditions female membership within territories of this group may be semi-permanent or permanent over extended periods (e.g., Estes, 1966 and 1969; Joubert, 1972; and David, 1973).

Whether these year-round territorial systems with one-male and permanent female groups are feeding or breeding territories is not clear from the work done to date. However, because the arid grassland and brushland habitats of the tsessebe (*Damaliscus lunatus*) and bontebok (*Damaliscus dorcas*) suggest food and water are scarce, they may also occupy feeding territories like the vicuna. The strong similarity between vicuna and sedentary Alcelaphinae appears to be a striking example of convergence in social organization by two unrelated and widely separated groups. I would suspect that both groups might be living under very similar ecological conditions.

Defecation-Urination and Scent Marking

Defecation-urination behavior had both social and environmental significance to the vicuna. Animals in all social groups eliminated only on traditional dung piles. Although the function of territorial defecation has long been assumed to be for territorial defense (warning outside animals away), there is a lack of evidence to support this view (Johnson, 1973). Dung piles within vicuna territories did not prevent outside groups from trespassing onto and using a site while an owner was temporarily absent. In Johnson's (1973) review of mammalian scent marking, he reported growing evidence for a number of functions within the same species and different functions between species. Johnson (1973, p. 522) gave the six most frequently proposed functions of scent marks, the third of which closely supports my observations as one of the important functions of this behavior for vicuna: "a system of labelling the habitat for an animal's own use in orientation."

It was vital that vicuna group members remain within their own territory or in familiar neutral areas to avoid attack from other territorial males. Vicuna communal dung piles were large and conspicuous throughout areas of usable habitat. Existing dung piles were used within newly established territories; unused sites were uncommon, and new ones were rare. Family group members appeared to use dung piles for their own orientation as an aid to remaining within safe and familiar areas (Franklin, 1971 and 1974). When a group left a safe area and trespassed onto another territory, it was the adult female members who were attacked and chased by the resident male. The rate of dung pile use (smelling, turning, positioning, etc.) greatly increased when animals approached their territorial boundaries, left the territory or moved through neutral areas: situations in which animals needed frequently to confirm their location. The greater anxiety of crias leaving, or being outside of familiar terrain was reflected by even higher rates of defecation-urination in these situations.

Members of the subfamily Alcelaphinae exhibit varying forms of scent marking behavior by preorbital gland secretions and by defecation on dung piles or central stomping grounds. However, a conspicuous difference from the vicuna is that only territorial male Alcelaphinae use dung sites while females and bachelor herd males eliminate wherever they happen to be. If self-orientation is a function of dung marking behavior in Alcelaphinae, it appears to apply only to adult territorial males.

My observations on vicuna male Defecation Urination Displays agree with Ralls' (1971, p. 449) statement that mammals appear to "mark frequently in a situation where they are both intolerant of and dominant to other members of the same species." The regular occurrence of exaggerated defecation-urination behaviors in conjunction with the male vicuna's territorial defense and aggressiveness to rivals suggested it was a form of threat display. The full role of male Defecation Urination Displays must yet be determined by measuring the responses of rivals to this behavior.

Although short-term primary functions of dung piles may have been intragroup orientation and territorial threat display, the behavior also caused major long-term effects upon the environment. The redistribution and localization of nutrients due to animals using the same dung piles over millennia of time have caused a localized acceleration of soil and plant succession. The resulting excrement influenced vegetation had deeper topsoil, greater water holding capacity, more nutrients and higher productivity than the adjacent vegetation types. The three successional stages of excrement influenced vegetation accounted for a fourth of the surface area of all plant communities. The climax stage (VT-1) covered 5 percent of the area, received 10 percent of all feeding use, produced 15 percent of the available forage and was a preferred vicuna forage. Environmental modifications that resulted from this behavior were favorable changes in the vicuna's habitat.

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