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Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia

Organización social, distribución y movimientos de una población migratoria de guanacos en la Patagonia chilena

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ABSTRACT

Herein we document the distribution, movement, and social organization of a guanaco (*Lama guanicoe*) population in a 25-km^2 area at Torres del Paine National Park in southern Chile. In 1980, the population was censused 28 times. Four socioecological periods were recognized: summer territorial, fall transitional, winter aggregational, and spring transitional. Family groups, male groups, solo males, mixed groups, and female groups were the major social units recognized. Guanacos spent the summer in the east region, migrating 12 km to the west region during winter. Family groups (53% of all animals), male groups (35%) and solo male (8%) were the main social units in summer, and mixed groups (80%) in winter. Snow cover and availability of forage were the suspected causes of seasonal migratory movements, that in turn greatly influenced social organization, group size, and composition.

Key words: group size, social units, sex ratio, migration, *Lama guanicoe*.

RESUMEN

En el presente artículo documentamos la distribución, movimiento y organización social de una población de guanacos (*Lama guanicoe*) localizada en un área de 25 Km^2 en el Parque Nacional Torres del Paine. La población fue censada 28 veces en 1980. Se identificaron cuatro periodos: verano territorial, otoño de transición, invierno de agregación y primavera de transición. Se reconocieron las siguientes unidades sociales: grupos familiares, grupos de machos, machos solitarios, grupos mixtos y grupos de hembras. Los guanacos permanecieron durante el verano en la región este, migrando 12 Km hacia el oeste durante el invierno. Durante el verano, los grupos familiares (53% de todos los animales), los grupos de machos (35%) y los machos solitarios (8%) fueron las principales unidades sociales, mientras que durante el invierno fueron los grupos mixtos (80%). La nieve y la disponibilidad de forraje fueron las posibles causas de los movimientos migratorios, los que a su vez influenciaron la organización social, el tamaño y la composición de grupo.

Palabras clave: tamaño de grupo, unidades sociales, razón de sexos, migración, *Lama guanicoe*.

INTRODUCTION

The guanaco *(Lama guanicoe)* is the most common and widespread aridland, wild ungulate in South America, ranging from northern Peru to central Chile on the dry west-facing slope of the Andes, across the Patagonia steppe, and southward to the wet forests of Tierra del Fuego. Guanaco populations were reported to be both sedentary and migratory. Guanacos have been observed migrating in Argentina (Prichard 1902) and Chile (Bridges 1957, Chapman 1977, Miller 1980). Raedeke (1979) found both types of populations in Tierra del Fuego and Jefferson (1980) and Franklin (1982, 1983) studied a sedentary population there. Despite these various reports and observations, no migratory guanaco population has been quantitatively studied or its social organization described.

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Torres del Paine is a National Park in southern Chile that encompasses about 250,000 ha from the Andean Cordillera to the Patagonian steppe (Fig. 1). Soon after the park was expanded in 1975, park guards conducted the first guanaco census and counted 97 animals in the Lago Pehoe sector. From 1975 to 1980, a series of censuses of the entire guanaco range were conducted, counting as many as 700 animals (J. Gonzales, pers. comm.). These initial censuses revealed that during summer, many guanacos were in Laguna Amarga sector, whereas during the fall and winter, most of the animals were in the Lago Pehoe sector. On the basis of these preliminary observations by park rangers, the guanaco population at Torres del Paine National Park was suspected to have been migratory, but information of movements and population structure was lacking.

This investigation was undertaken to document distribution and seasonal movement patterns of the guanaco population at Torres del Paine National Park. Specific objectives were to: determine to what degree this population was migratory, determine what social units existed, and assess the seasonal distribution and movements of social units.

Study Area

Torres del Paine National Park (Region XII, 51°3' S, 72°55' W) is located in the eastern foothills of the Andean Mountains on the western edge of the Patagonia. The 25.5-km^2 study area in the center of the park was bordered by lake Nordenskjold to the north and west, lakes Sarmiento and Pehoe to the south, and lakes Larga and Cisnes to the east. Elevation ranged from 130 m to 535 m.

To enable a better understanding of guanaco movements and distribution, the study area was divided into three nearly equally sized units: the west region (8.53 km^2) contained a mountainous terrain of low valleys to the highest peaks within the study area; the central region (8.46 km^2) was characterized by hilly terrain with several transverse depressions; and the east region (8.47 km^2), flattest of the three regions, contained few hills but numerous lagoons and ponds (Fig. 1).

General climatological periods at Torres del Paine include a warm, windy, rainy season from October through April and a cold, relatively dry season with little wind, lasting from May through September. Austral spring is characterized by high-velocity westerly winds creating cold but dry conditions; summer is windy with occasional rain; fall is often foggy and cold; and winter is cold to freezing, calm, and with or without snow. Average annual precipitation at Guarderia Pudeto located in the west region is 546 mm; 60% usually falls between January and May. In 1980, there was moderate snow cover (300-700 mm) from mid-June to the end of August. Mean annual minimum and maximum temperatures at Laguna Amarga (4 km E of the study area) between 1968 and 1972 were 5.7 °C and 10.2°C (Pisano 1974).

The vegetation of Torres del Paine was characterized by shrubs and grasses (Ortega 1985, Ortega & Franklin 1988). Pisano (1974) described it as a xeric pre-Andean shrub association. The dominant species in this plant association was *Mulinum spinosum* a spiny, 10-50-cm-high dome-shaped shrub. Valleys and depressions usually contained the shrubs *Senecio patagonicus* and *Adesmia boronoides*. Highly exposed areas were characterized by *Acaena* sp., *Calceolaria* sp., and *Azorella caespitosa*. *Rumex acetocella* is very common in disturbed sites such as roadsides. Successional meadows and pond littoral zones are dominated by the grasses *Holcus lanatus* and *Hordeum comosum* with the shrub *Berberis buxifolia* typically found on the periphery. The only tree present is *Nothofagus antarctica*.

METHODS

The population was censused 28 times from January to December 1980. Each census was completed in 2 consecutive days: on the 1st day, a 7.5-km fixed route was walked through the western region, and the 2nd day, a 12.2-km route was traveled through the rest of the area with the aid of an all-terrain cycle for road travel. Guanacos in the central and eastern regions were censused on foot from major peaks. This standardized route was

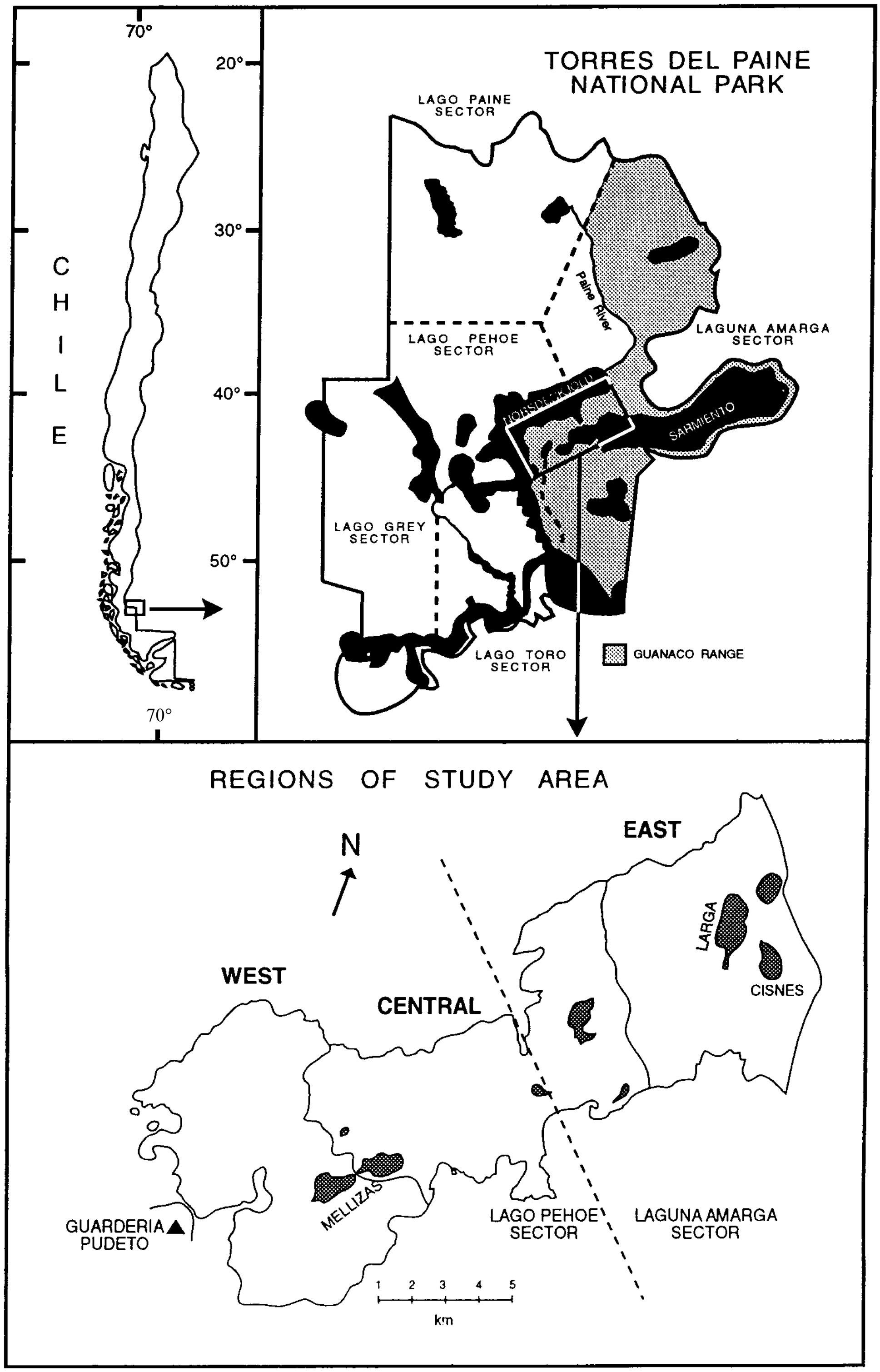

Fig. 1: Study area at Torres del Paine National Park in southern Chile showing the West, Central, and East Regions.

Area de estudio en el Parque Nacional Torres del Paine al sur de Chile mostrando las regiones Oeste, Central y Este.

designed to include the same hills from which animals could be observed in the immediate vicinity, cover all the terrain, and avoid duplication. Binoculars (8 x 10) and spotting scopes were used for observation. Censuses were from 08:00 and 15:00 h.

Group size, sex, age, type of social unit, and location were recorded on aerial photos. Age classes were adults (2 years and older), yearlings (>1<2 years old), and young of the year (chulengos). Because of the large number of animals in some winter groups and the difficulty of determining sex of individuals of this sexually monomorphic species, sex composition was estimated by the ratio of individual males and females identified by defecation-urination postures and genital organs.

Data were analyzed by analysis of variance in which significant differences between means were determined by the protected least significant difference multiple-comparison procedure (Snedecor & Cochran 1967). All significance levels are reported from two-tailed tests ($P = 0.05$).

RESULTS

General Social Organization

We found the following general socioecological periods that describe changes in social organization and population distribution: summer territorial (SUT), fall transitional (FT), winter aggregational (WA), and spring transitional (SPT). Within those periods social units were identified: family groups (FGs), male groups (MGs), solo males (SMs), mixed groups (MXGs), and female groups (FEGs). Family groups were composed of an adult male, adult females, and young <15-months old. Male groups were composed of immature and mature nonterritorial males. Solo males were mature males either with a territory or seeking one, but without females. Mixed groups included both sexes and all age classes. Female groups were mature females, with or without young of the year, or yearling females alone or in groups, but never with a male.

The SUT period was the longest of the socioecological periods, spanning from mid-October to the end of March. This was the reproductive season in which birth and mating occurred. Social units present during this period were: FG (35% of all social units observed), MG (15%), SM (42%), and FEG (8%)(Fig. 2a). During the SUT period individuals were mostly found in FGs and MGs (Fig. 2b). During this time, territorial males were seen defending an area from intruders such as MGs, SMs, and sometimes females.

The FT period was short, lasting from early April to late May. Guanacos started migrating to the west in the same social units already mentioned (Fig. 2a). As during the SUT period, animals were found mainly in FGs and MGs (Fig. 2b).

The WA period extended from early June through the third week of August. The main social units were MXGs (39%) and FEGs (41%, Fig. 2a), but most animals (80%) were in MXGs (Fig. 2b).

The SPT period started by late August and ended in mid-October. All social units were found, with SMs being the most common social unit (48%, Fig. 2a). Equal proportions of animals, however, were found in FGs, MGs, and MXGs (Fig. 2b).

Guanaco Density and Distribution

The number and density of guanaco social units, a measure of social organization and social behavior, changed from one season to the next (Table 1). During the SUT (1.5 gps/km^2) and FT periods (1.2 gps/km^2) the density of social units was higher than during the WA (0.8 gps/km^2) and SPT periods (0.9 gps/km^2). The only significant differences in group density, however, were between SUT and WA, and SUT and SPT periods. Larger group size during WA resulted in lower group density compared to SUT.

During the SUT period, most guanaco groups were in the central or east regions. Group density in the west (0.9 gps/km^2) was significantly lower compared with the other regions. During the FT period, no significant difference of group density was found among the regions, although most of the groups were found in the central or west regions. By the WA period, groups moved to the west region (1.4 gps/km^2), with the lowest group

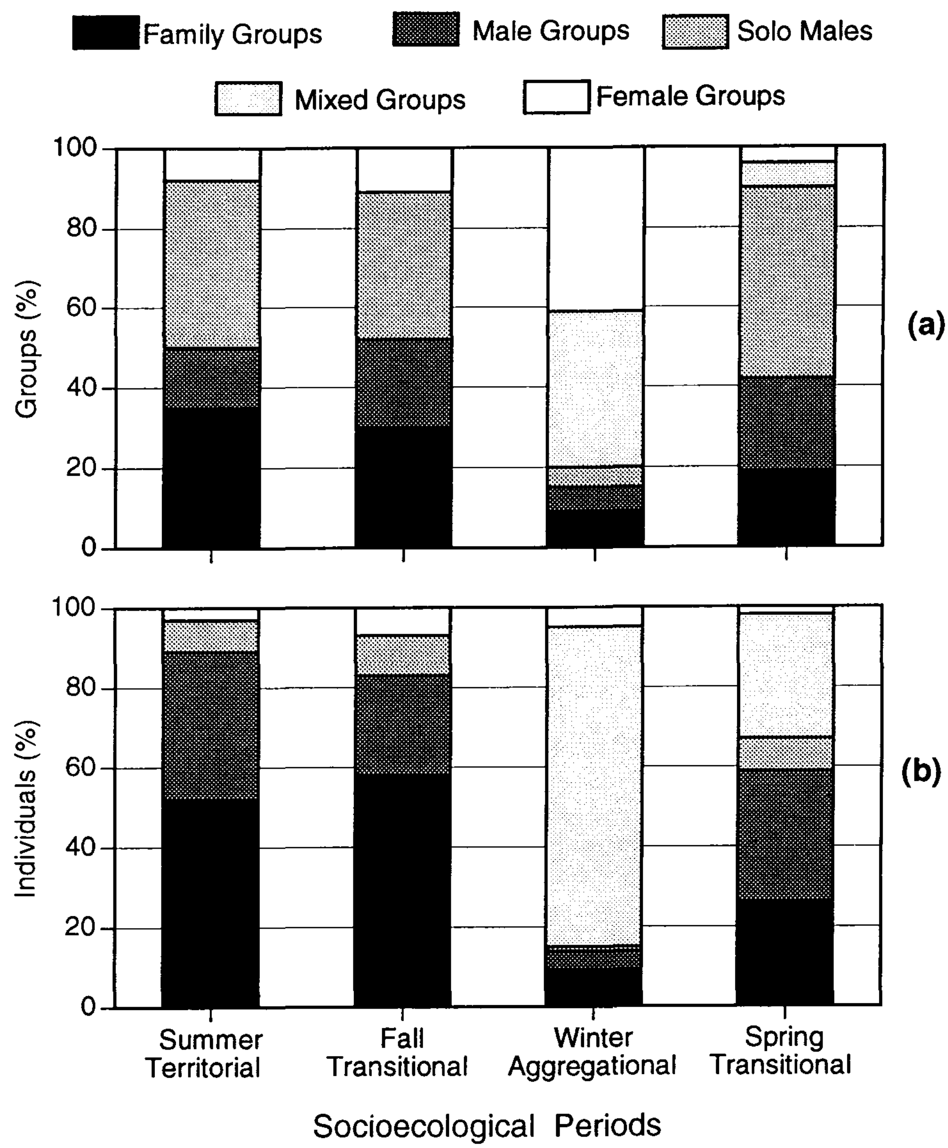

Fig. 2: Percent of different types of (a) social groups and (b) individuals in social groups by socioecological periods, Torres del Paine National Park, Chile.

Porcentaje de los diferentes tipos de (a) grupos sociales y (b) individuos en los grupos sociales en los períodos socioecológicos, Parque Nacional Torres del Paine, Chile.

density found in the east (0.4 gps/km^2). Finally, by the SPT, groups moved back to the central and east regions, and the west region had the lowest group density (0.4 gps/km^2) as during the SUT period.

During the SUT (7.9 an/km^2) and WA periods (7.4 an/km^2), animal density was greater than in the FT (4.7 an/km^2) and SPT periods (5.6 an/km^2). Animal density in the FT period was significantly less than in the SUT and WA periods.

The highest animal density in the SUT season was in the east (15.4 an/km^2) and lowest in the west region (1.9 an/km^2; Fig. 3a). During the FT period, animals moved westward and were distributed more evenly throughout the study area (Fig. 3a). By the WA period, guanacos had moved to the west region (15.3 an/km^2), and the east region then had the lowest density (2.9 an/km^2). During SPT, guanaco distribution again was scattered as the animals moved from west to

TABLE 1

Annual density of guanaco social units by region at Torres del Paine National Park, Chile, 1980. Mixed groups based upon winter and spring socioecological periods only

Densidad anual de las unidades sociales del guanaco por regiones en el Parque Nacional Torres del Paine, Chile, 1980. Los grupos mixtos están basados en los períodos socioecológicos del invierno y primavera solamente

Social units	Regions			
	West	Central	East	Total
Family groups				
Groups/km²	0.12	0.38	0.55	0.35
Animals/km²	0.64	2.39	5.14	2.72
Male groups				
Groups/km²	0.16	0.20	0.24	0.20
Animals/km²	0.62	1.37	4.24	2.07
Sólo males				
Groups/km²	–	–	–	–
Animals/km²	0.37	0.68	0.36	0.47
Mixed groups				
Groups/km²	0.21	0.14	0.08	0.14
Animals/km²	4.58	2.66	2.31	3.16
Female groups				
Groups/km²	0.14	0.13	0.11	0.13
Animals/km²	0.21	0.22	0.27	0.23
Total				
Groups/km²	1.01	1.34	1.03	1.12
Animals/km²	5.74	5.26	8.31	6.46

east to occupy their SUT breeding range (Fig. 3a).

Density and distribution of FGs varied throughout the year, following patterns similar to those described for the total population. During the SUT period, mean FG density was 0.5 groups/km^2, greatest in the east (0.8 gps/km^2), and lowest in the west (0.18 gps/km^2; Fig. 3b). By the FT period, mean FG density was 0.4 groups/km^2, with no significant difference among the regions. FG density was lowest during the WA period (0.1 gps/km^2), and again, with no differences between the regions. During the SPT period, FG density (0.2 gps/km^2) began to increase, especially in the east region, with the west region significantly lower than the other regions.

Density of animals in FGs ranged from 0.7 an/km^2 during the WA period to 4.7 an/km^2 in summer with a year-round mean of 2.7 an/km^2. Seasonal distribution in the three regions followed the same trends as for the density of FGs.

Year-round MG density was 0.20 gps/km^2 with no significant differences between regions (Table 1). Density of MGs during the SUT and SPT periods was the same (0.2 gps/km^2). In SUT there were no significant differences of MG density between regions, but in SPT, the MG density was higher in the east (0.3 gps/km^2) than in the west region (0.07 gps/km^2; Fig. 3b). In the FT period, MGs moved to the west and central regions. Because most males were in the MXGs during the WA period, MG density drastically declined to 0.05 gps/km^2, with no significant differences between regions. Density of animals in MGs ranged from 0.4 an/km^2 during the WA period to 2.9 an/km^2 in SUT, with a year-round mean of 2.1 an/km^2. Seasonal distribution in the three regions followed a trend similiar to the group density of MGs.

Density of Solo Males was significantly higher in the central region during the SUT (0.9 an/km^2) and FT periods (0.9 an/km^2; Fig. 3b). In WA period, Solo Males joined the MXGs, resulting in a low SM density of only 0.04 an/km^2, with no difference between regions. In the SPT period, SM density increased to 0.5 an/km^2, with the central region again the highest (0.6 an/km^2), but no significant difference between the three regions.

Guanaco males ceased defending territories during the WA period, whereas the majority of females joined MXGs. In winter, MXG density (0.3 gps/km^2) was greatest in the west (0.6 gps/km^2) and least in the east region (0.1 gps/km^2; Fig. 3b). By the SPT period, MXGs density declined to 0.05 gps/km^2, with no significant differences between regions (Fig. 3b). Density of animals in MXGs was greatest during WA period in the west region (13.6 an/km^2).

Group density of female groups ranged from 0.04 gps/km^2 during the SPT to 0.3 gps/km^2 in the WA period, with a year-round mean of 0.1 gps/km^2. No seasonal differences of group density in FEGs were found between the three regions. Year-round density of animals in FEGs was 0.2 an/km^2,

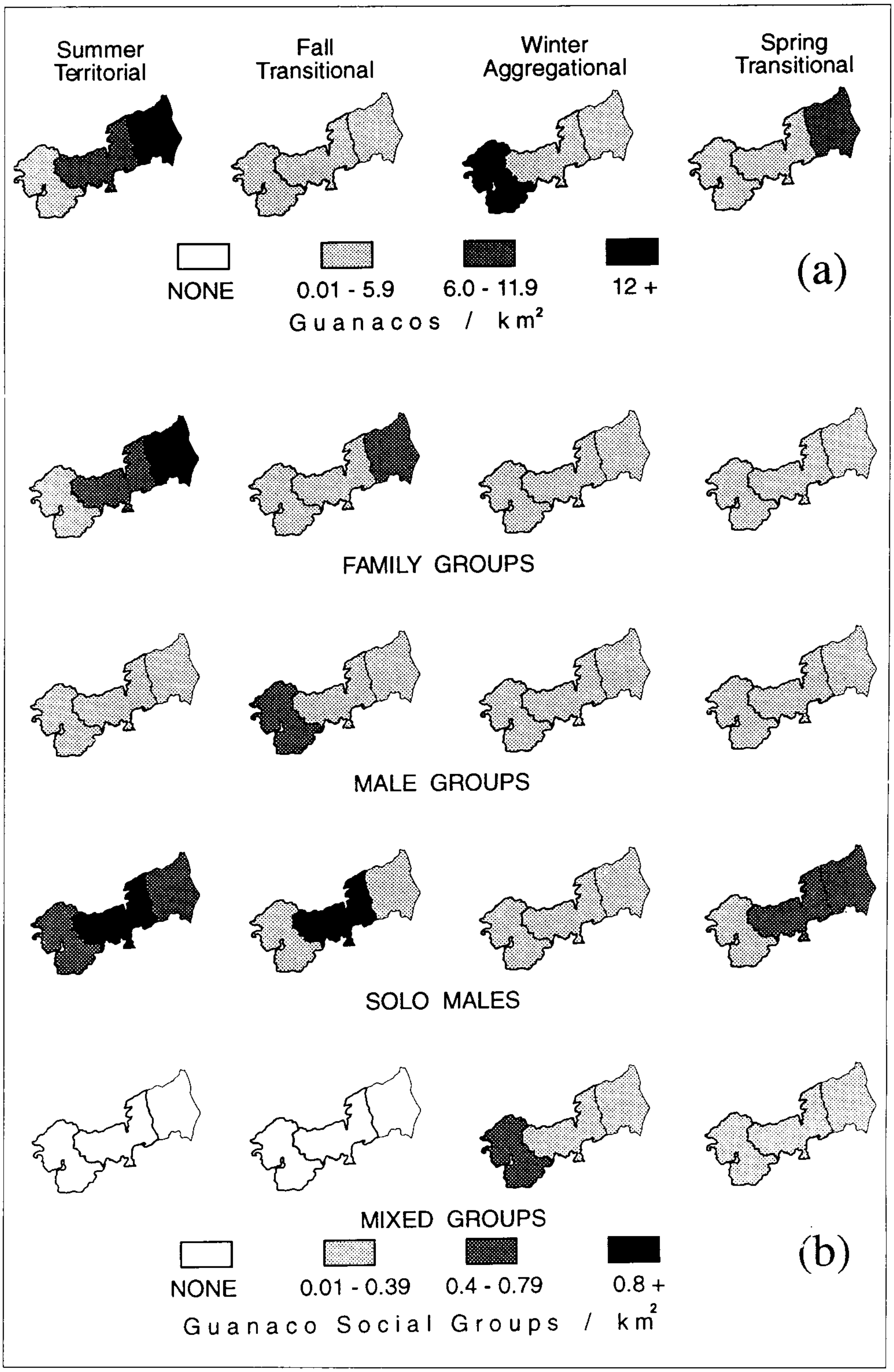

Fig. 3: Regional (a) animal and (b) social group density during the annual socio-ecological periods, Torres del Paine National Park, Chile.

Densidad regional de (a) animales y (b) grupos sociales durante los períodos socioecológicos, Parque Nacional Torres del Paine, Chile.

ranging from 0.1 an/km^2 during SPT to 0.4 an/km^2 in the WA period, again, with no seasonal differences of density of animals in FEGs between the three regions. FEGs were a transitional social unit of short duration when females moved from FGs to MXGs or vice versa. The greater density of FEGs during the WA was most likely the result of unmated females moving from the western winter range to the eastern summer range.

Group Size and Composition

Guanaco group size and composition was greatly influenced by migratory movements and social group instability. FG size varied from week to week. Group size was largest in the east and smallest in the west and similar for the SUT, FT, and SPT periods. Year-round FG size averaged 7.9 an (Table 2), with no significant differences between seasons.

MG size during the SUT was largest in the east (22.2 an) and smallest in the west region (3.0 an), with 7.7 an in the central region. No MGs were found in the east region during the FT period, and there was no significant difference in MG size between the west (5.3 an) and the central regions (2.4 an). There were not enough data to analyze MG size in WA period by regions. The SPT period followed the same MG size trend as in SUT, with no significant difference between the three regions.

The largest average MXG size occurred in the SPT ($\bar{x}$ = 31.6 an, range = 3 - 84) and, the smallest, in the WA period ($\bar{x}$ = 19.0 an, range = 2 - 173; Table 2), with no difference in MXG size between the three regions. MXG size was larger (22.0 an) in the west region during the WA period and smaller toward the east region (9.7 an), but had no significant difference between the three regions during the WA and SPT periods.

Little change of FEG size was observed. Yearly FEG size ranged from 1.0 to 3.3 an (Table 2) and averaged smaller in WA period (1 an) than the other periods. Regional analysis showed that FEG size in the east region was larger than in the other two regions. FEG size was uniform throughout the seasonal and regional analysis.

TABLE 2

Guanaco social group size by season at Torres del Paine National Park, Chile, 1980. (*SE* = standard error; n = number of groups)

Tamaño de los grupos sociales del guanaco por estación en el Parque Nacional Torres del Paine, Chile, 1980. (*SE* = error estándar; n = número de grupos)

	Sociecological Periods				
Social units	Summer	Fall	Winter	Spring	Year-round
Family groups					
mean	7.87	7.24	8.75	8.03	7.85
range	2-38	2-40	3-15	2-18	2-40
SE	0.50	1.27	1.35	0.73	0.40
n	175	29	8	37	249
Male groups					
mean	13.54	4.29	8.20	8.77	10.52
range	2-135	2-15	2-16	2-82	2-135
SE	2.52	0.83	2.42	2.26	1.49
n	2	21	5	43	141
Mixed groups					
mean	–	–	18.97	31.63	22.14
range	–	–	2-173	3-84	2-173
SE	–	–	5.45	7.78	4.56
n	–	–	33	11	44
Female groups					
mean	2.16	2.50	1.06	3.26	1.86
range	1-7	1-5	1-2	1-11	1-11
SE	0.27	0.34	0.04	1.30	0.17
n	38	10	35	7	90

Sex Ratio and Mortality

The overall sex ratio (guanacos 1 year and older) was measured as 41% females: 59% males, with no significant difference between periods (Table 3). During the SUT season, more than 70% of all males 1 year old and older were found in MGs, with the rest of the males evenly distributed in FGs and as SMs (Fig. 4a). By the FT period, there was an increase in the percentage of males seen in FGs and SMs, although 50% of the males were still in MGs. During the WA period, 85% of the males were in MXGs, and the balance in MGs, FGs, or SMs. By the SPT, 55% of the males were found in MGs and only 20% in MXGs.

Females were found in FGs, FEGs, and MXGs. In the SUT period, more than 90% of the females were in FGs (Fig. 4b). During the FT period, more females were found in FEGs than during the SUT period. By the WA period, over 70% of the females also

TABLE 3

Seasonal sex ratio of guanacos 1 year and older at Torres del Paine National Park, 1980. (n = number of census)

Razón de sexos por estación en los guanacos mayores de un año en el Parque Nacional Torres del Paine, 1980. (n = numero de censos)

Socioecological Periods	n	Males (%)	Females (%)
Summer	13	60	40
Fall transitional	3	51	49
Winter Agregational	4	55	45
Spring transitional	8	63	37
Overall	28	59	41

moved into MXGs. Females began returning to FGs in the SPT season.

Altogether, 47 guanaco carcasses were found in the 25.5-km^2 study area: 42% in the central region, 30% in the west and 28% in the east. Carcasses of adult females (32%), adult males (30%), and chulengos (30%) were found in equal proportions (8% of the adult carcasses could not be sexed). Regional analysis by sex show that 50% of the male carcasses were found in the central region, 29% in the east, and 21% in the west region. Of the female carcasses, 47% were found in the west region, 40% in the central, and 13% in the east region. The highest numbers of chulengo carcasses were found in the east (50%) and were similar for the central (29%) and eastern (21%) regions.

Causes of death were unknown, but predation by the Patagonia puma (*Felis concolor*) was suspected to be an important cause of guanaco mortality in the park (Wilson, 1984). Fifty-five percent of our 11 sightings of pumas were in the central region, the same area where we found the most carcasses. The high percentage of chulengo carcasses in the east correlated with the greatest distribution of FGs with their newborn chulengos there in the SUT birth season. The only time females were in the west region was during the WA period in MXGs. Why there might have been different mortality of females on the WA range is unknown.

DISCUSSION

Migration has been defined as regular round trips of animals within a life-span of the individual (Sinclair 1983). Based on this definition, the population of guanacos at Torres del Paine National Park appeared to be migratory. The round trip was in this case an annual event when most guanacos spent the summer in the east, moved 12 km to the west region for the winter, and returned to the east the next spring (Fig. 5).

Baker (1978) recognized "facultative" and "obligatory" migration. Facultative migration occurs when an animal initiates migration in response to a currently adverse situation (e.g., overcrowded, food shortage). Obligatory migration is usually at a fixed time of a year without reference to habitat suitability. Movements of guanacos at Torres del Paine National Park appeared to be a facultative migration probably in response to adverse weather, especially snow, and shortage of food resources in the east as meadows became snow covered and MXGs moved westward where there was a greater abundance of browse (Ortega & Franklin 1988). Less wind and shallower snow may also help to explain why the population moved west. In such a strongly seasonal and patchy environment (Dingle 1980) as Torres del Paine with sharp changes in climatic and habitat conditions, migration is clearly an adaptive response.

For FG males, the east-open country may have been more useful than the hilly terrain of the west region in maintaining control over territories. For females in this region, especially those with chulengos, would be more advantageous in detecting predators such as pumas or stray dogs (*Canis familiaris*) that had wandered into the Park from nearby sheep ranches. The east region also had better habitat: the highest percentage of meadow, a highly productive habitat type (Ortega & Franklin 1988).

In the east region, where there was high competition for territories, stronger males presumably obtained the better sites on which they attracted and defended females. Thus, males that could not obtain a territory in the east region were believed to be displaced toward the central region. However, it would be unfavorable for females with newborn to join males in such an area because, topographically, the central region ravines and steep slopes did not favor detection of predators. Better food resources

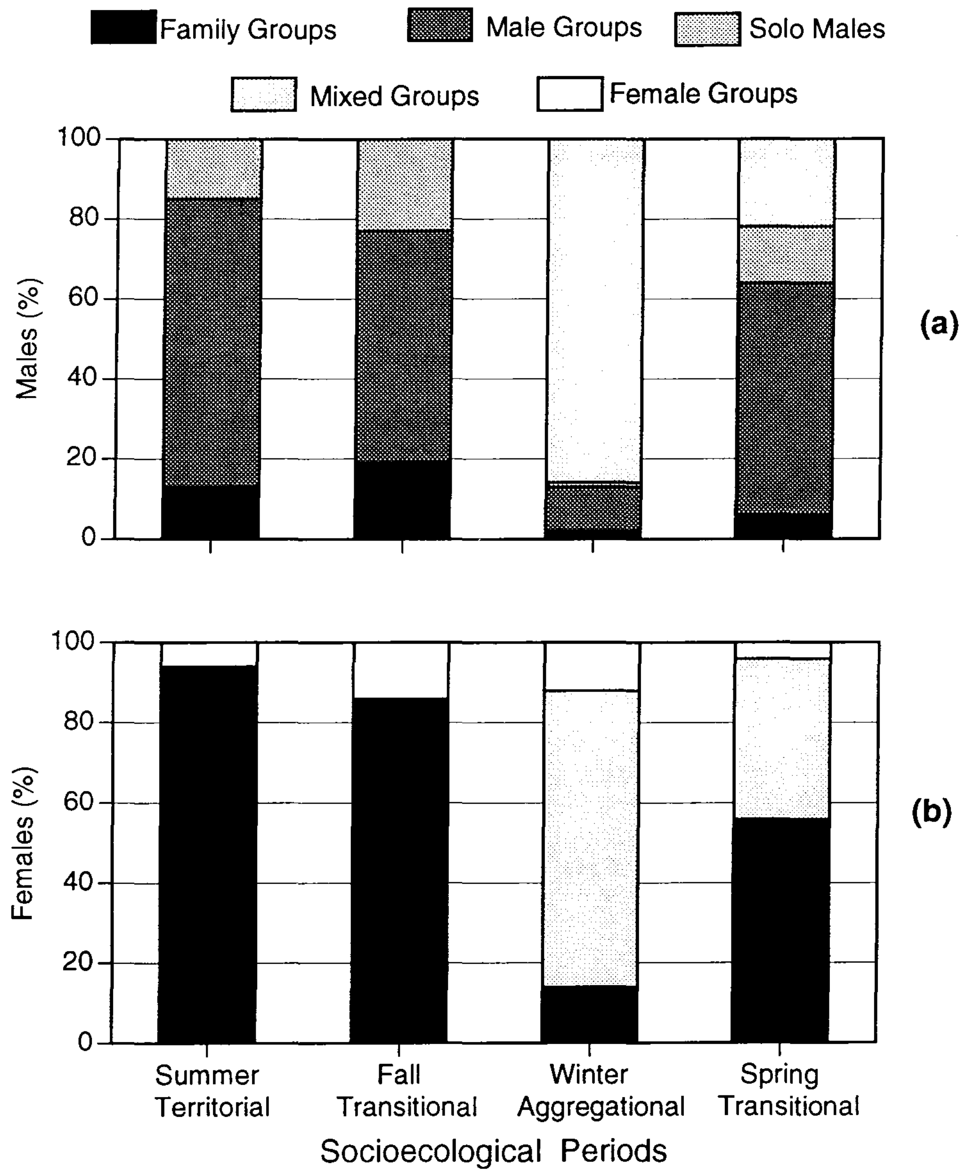

Fig. 4: Percent distribution of guanaco (a) males and (b) females (1 year and older) in social groups by socioecological periods, Torres del Paine National Park, Chile.

Porcentaje de la distribución de los guanacos (a) machos y (b) hembras (de un año y mayores de un año) en los grupos sociales en los períodos socioecológicos, Parque Nacional Torres del Paine, Chile.

during the SUT also were believed to have attracted MGs to the east region. Perhaps because MGs were highly mobile and without territories, they were the first guanaco social unit to move to the west region for the WA period.

Social ungulates gain protection from predators by forming groups; however, group size is limited by competition for food (Wittenberger 1981). In Torres del Paine, small group size would be expected during the summer territorial season to provide the best resources to females, yearlings and chulengos. During the summer, competition for food would not have allowed formation of excessively large groups, whereas during WA period, the risk of predation as increased by snow and social isolation would have favored large group size. Although family and male group size did not vary throughout

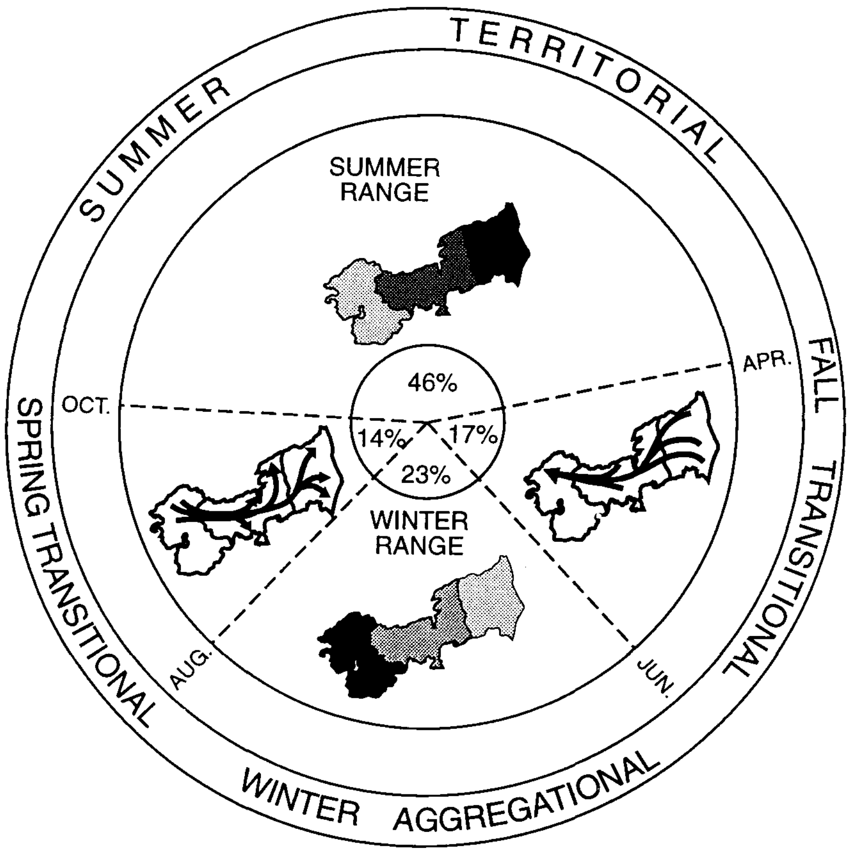

Fig. 5: Guanaco year-round socioecological periods and movements. Lenght of time of each period shown as percentage in the center of circle.

Períodos socioecológicos y movimientos del guanaco. El tiempo de cada período se muestra como porcentaje en el centro del círculo.

the year, large mixed groups that formed for the winter offered advantages of greater predator detection in the central and east regions, where pumas were common.

After this research project, the same annual cycle of guanaco movements has been observed, with slight variations from one year to the next in the timing of the fall and spring transitional periods as influenced by the weather (Franklin et al. unpubl. data). Snow storms and snow cover have been especially important in triggering sudden movements to the west.

Knowledge of social organization is an integral and inseparable component when managing guanaco populations. If the guanaco is to be used as a renewable resource as proposed (Franklin & Fritz 1991), male groups that play an important role in the ontogeny of guanaco social behavior (Wilson & Franklin 1985) must be considered, not just a potential biological surplus, but also as the backbone of any guanaco population. It is essential to maintain the social integrity of male groups and their relationship to solo males and family groups for the normal succession and replacement of territorial males. Understanding the annual cycle of social organization and movements of a given population will be essential tools for future conservation and management of the South American guanaco.

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