

Development of juvenile guanaco social behavior: first study on a wild population from the Chilean Patagonia

Desarrollo de la conducta social de guanacos juveniles:
primer estudio sobre una población silvestre en la Patagonia Chilena

GLADYS GARAY¹, WILLIAM L. FRANKLIN^{2, 3},
RONALD J. SARNO^{2, 3} AND WARREN E. JOHNSON^{2, 3, 4}

¹Departamento de Ecología, Universidad Católica de Chile, Santiago, Chile

²Centro de Investigación de Vida Silvestre Patagónica, Parque Nacional Torres del Paine, Puerto Natales, Chile

³Department of Animal Ecology, 124 Science II, Iowa State University, Ames,
IA 50011 USA (Send reprint requests to WLF)

^{2, 3, 4}Laboratory of Viral Carcinogenesis, National Cancer Institute, Frederick, MD 21701 USA

ABSTRACT

The development of social behavior in juvenile guanacos (chulengos) was studied by focal animal observation in Torres del Paine National Park for one annual cycle. This is the first study of its kind on a free ranging, wild population of guanacos. Birthing, mating, expulsion, formation of winter groups, and migration were key events influencing chulengo social development. The highest rate of alarm behavior occurred in January when chulengos were one month old. The percentage of chulengos nursing/hr decreased from a high of 56% in January to a low of 10% in July and 0% in September. There was no difference between the sexes in duration of nursing during summer or fall, but in winter chulengo males nursed more. Amount of time spent in different activities varied between summer and winter: feeding increased from 30% to 93% while resting decreased from 50% to 25%, walking from 12% to <5%, and playing decreased from 5% to 0%. Chulengos showed submissive behavior towards adult males throughout the year, with significant peaks in May when in Mixed Groups and in November during expulsion from the Family Group.

Key words: *Lama guanicoe*, juvenile, social behavior, Chile.

RESUMEN

Estudiamos el desarrollo de la conducta de chulengos por un año en el Parque Nacional Torres del Paine. Este es el primer estudio de este tipo hecho con una población de guanacos en vida libre. Los sucesos principales que influyen el desarrollo social del chulengo son el nacimiento, el cruzamiento, la expulsión, la formación de grupos de invierno y la migración. La tasa más alta de conducta de alarma fue durante enero cuando los chulengos tenían un mes de edad. El porcentaje de chulengos amamantando por hora bajó de 56% en enero a 10% en julio y a 0% en septiembre. No encontramos diferencias entre sexos en la duración de amamantamiento durante el verano y otoño, pero en el invierno los chulengos machos amamantaron más. El tiempo gastado en diferentes actividades varió entre verano e invierno: alimentarse aumentó de 30% a 93%, descansar bajó de 50% a 25%, caminar de 12% a < 5%, y jugar de 5% a cero. Los chulengos fueron sumisos con los machos adultos durante todo el año con aumentos significativos en mayo cuando estaban en grupos mixtos y en noviembre durante el período de expulsión del grupo familiar.

Palabras clave: *Lama guanicoe*, chulengo, juvenil, conducta social, Chile.

INTRODUCTION

The development of social behavior in juvenile mammals has a strong influence on their immediate survivorship and ultimately their reproductive fitness. Although juvenile social behavior and inter-relationships established with other individuals are expected

to have life-long consequences, development of wild ungulate social behavior is poorly understood. Most studies have focused on specific behaviors and have not been from a broader holistic perspective in a natural setting (Altmann 1960, Clutton-Brock & Guinness 1975, Estes & Estes 1979, Fagen 1981).

The development of social behavior in juvenile guanacos (*Lama guanicoe*), the dominant arid-land wild ungulate of South America (Franklin 1982) has not been studied in a free-ranging wild population. Social organization of the guanaco is based upon resource defense polygyny, during the spring and summer (Franklin 1983, Jurgensen 1985, Franklin & Fritz 1991). During their first year, juvenile guanacos (chulengos) spend the summer territorial season (when adult males are actively defending territories) and the fall and spring transitional seasons (when males leave their territories in the fall and when they arrive back to their territories in the spring) with their mothers in Family Groups (comprised of 1 adult male, numerous adult females and their young), and are found mostly in Mixed Groups (consisting of adult males, adult females and their young) during the winter (Franklin 1982 & 1983, Ortega 1985, Garay 1986, Ortega and Franklin 1995). As they approach one year of age chulengos are expelled from their Family Groups by the adult territorial male (Franklin 1983). Expelled yearling males join Male Groups and yearling females join Family Groups. Thus, much of the guanaco's social development takes place within the Family Group during its first year of life.

The goal of this study was to document the behavior of free-ranging juvenile guanacos. Our specific objectives were to: 1) quantify changes in juvenile activities and behavior relative to seasonal and social organizational changes, and 2) assess whether there were differences in the development of social behavior between juvenile males and females.

STUDY AREA

This study was conducted in Torres del Paine National Park, Chile (51° 3'S, 72° 55'W). The 22.5 km² study area was between Lakes Sarmiento and Nordenskjold (the Peninsula) during spring and summer, and the eastern sector of Lake Pehoe in fall and spring. The open landscape ranges from meadows to steep hills, with elevations ranging from 50-500 m. Pisano (1974) classified the vegetation as a dry pre-Andean shrub

association dominated by "mata barrosa" (*Mulinum spinosum*). In successional ponds and meadows ("vegas") *Holcus lanatus* and *Hordeum comosum* were common. Patches of the shrub "calafate" (*Berberis buxifolia*) and groves of "nirre" (*Nothofagus antarctica*) and "lenga" (*Nothofagus pumilio*) trees were scattered throughout the study area.

Two major climatic seasons mark this region. The cool summer was from December to February and had an average maximum temperature of 19.7° C (January), average precipitation of 102 mm, and typically strong westerly winds. Winter, from June to August, was cold with an average temperature of -5.3° C (July), an average precipitation of 21 mm, and little wind (see Ortega & Franklin 1988, Johnson et al. 1990 for additional description). Between the longest day in the summer and shortest in winter there was a difference of 8.9 hr of daylight.

METHODS

Field work was conducted for one complete annual cycle from 10 January 1983 to 6 January 1984. From October through March 6 hr of observations were made for 20 days / mon between 0900 and 1900 hr. From April to September 6 hr of observations were made 21 days/mon between 1100 and 1700 hr.

Data were collected by focal animal sampling (Altmann 1974) on 1) social interactions of chulengos with other group members, 2) time-activity budgets of chulengos, and 3) nursing by chulengos. The first chulengo to be observed was randomly selected, then data were collected for 15 min for each of the three data-types (for a total of 45 min) before repeating the process for the next chulengo. Thus, every field day, information was gathered for each data type during 8 observation periods that lasted 15 min each (i.e. 2 hr/day/data type). Originally, the frequency of 10 types of social interactions were monitored (Garay 1986), but only aggression, submission, play, and nursing are reported here. The time-activity budget for the focal animal was assessed by measuring the duration of feeding, nursing, resting, walking, playing, and submission.

During the nursing observation period, the duration of nursing for all chulengos within the group was monitored.

Data were gathered on chulengos from several known Family Groups identified daily by location, group composition, and known animals. The mean daily number of chulengos observed was 4.5 in January, 7.0 in March, 5.4 in May, 9.3 in July, 10.3 in September, and 10.4 in November. In addition, a group with one chulengo was observed from March through November to compare the behavior of a single juvenile. Throughout the year, groups with > 1 chulengo were observed for 3 wks/mon and groups with 1 chulengo for 1 wk/mon. Chulengos were observed from 5-200 m with binoculars and a spotting scope. For some selected individual and social behaviors, only data for every other month beginning in January were analyzed and reported. Data from social interactions, time activity budgets, and nursing were analyzed using t-tests, chi-square analysis, and analysis of variance (SAS, Institute Inc. 1989).

RESULTS

In January and February, Family Groups were located in the eastern portion of the peninsula study area. In March, females and young started moving between territories of adult males, and by May mixed groups formed and migrated 10 km west to Paso de la Muerte. In August, they began their movement eastward and became established in relatively stable Family Groups by October (see Ortega and Franklin 1995).

The expulsion of chulengos by adult males occurred between 3 September and 9 December 1983. The birth season began 19 November and extended until the end of January, with 49% of the chulengos born by 1 December. The breeding season was from 9 December to the end of February.

When chulengos were confronted by strange objects and disturbances, they often became alarmed and retreated. The highest rate of alarm behavior occurred in January (rate = 0.18/hr), when chulengos were one month old, and declined to zero in July. The smelling of other animals (olfaction) by chulengos followed a similar pattern, with

the highest rate in January (0.23/hr) and declining to 0% in July.

Other animals showed aggressive behavior towards chulengos year-round, with the highest rate (0.21/hr to chulengo females) occurring in March when chulengos began mixing with strange adult females and chulengos in Mixed Groups. The difference in the frequency of submissive behaviors by males and females was only significant in March ($F = 2.12$, $P < 0.05$, $d.f. = 1,8$), when female chulengos received more aggression than males. Chulengos were most commonly separated by a distance of 3 m (most frequent distance-class) from their mothers and 20 m from the territorial male.

The percentage of chulengos nursing/hr decreased from a high of 56% in January to 10% in July and 0% in September (Fig. 1). Chulengos nursed once/2 hr in January ($n = 40$ hr of observation), once/2 hr in March ($n = 40$), once/3 hr in May ($n = 30$), once/12 hr in July ($n = 30$), and no nursings were observed in September ($n = 30$), October, or November ($n = 40$). There was no seasonal difference in the duration of nursings between summer and fall, but in winter it declined (Fig. 2). There was no difference between the sexes in duration of nursing in summer or fall, but in winter chulengo males ($x = 132$ sec/hr, $S.E. = 10.8$, $n = 5$) nursed significantly more ($T = 2.9$, $d.f. = 8$, $P = 0.0189$, $n = 10$) than females ($x = 110$ sec/hr, $S.E. = 12.4$, $n = 5$).

Chulengos initiated more nursings as they grew older, and mothers increasingly terminated the nursing bouts (Fig. 3). Mothers also rejected fewer nursing attempts as chulengos increased in age (Fig. 4), females were rejected fewer than males in late fall ($F = 2.33$, $P < 0.05$, $d.f. = 1,8$). At near significance, female chulengos initiated nursings more than male chulengos ($X^2 = 5.66$, $d.f. = 2$, $P = 0.059$, $n = 87$).

Time spent feeding increased from January (30% of the time) to mid July (93%) ($F = 31$, $P < 0.01$, $d.f. = 1,8$) (Fig. 1). Male and female chulengos grazed the same amount of time during all seasons, except in fall when males fed an average of 728 sec/hr ($S.E. = 221$, $n = 212$) and females 802 sec/hr ($S.E. = 175$, $n = 227$) ($T = 3.86$, $d.f. = 437$, $P = 0.0001$, $n = 439$).

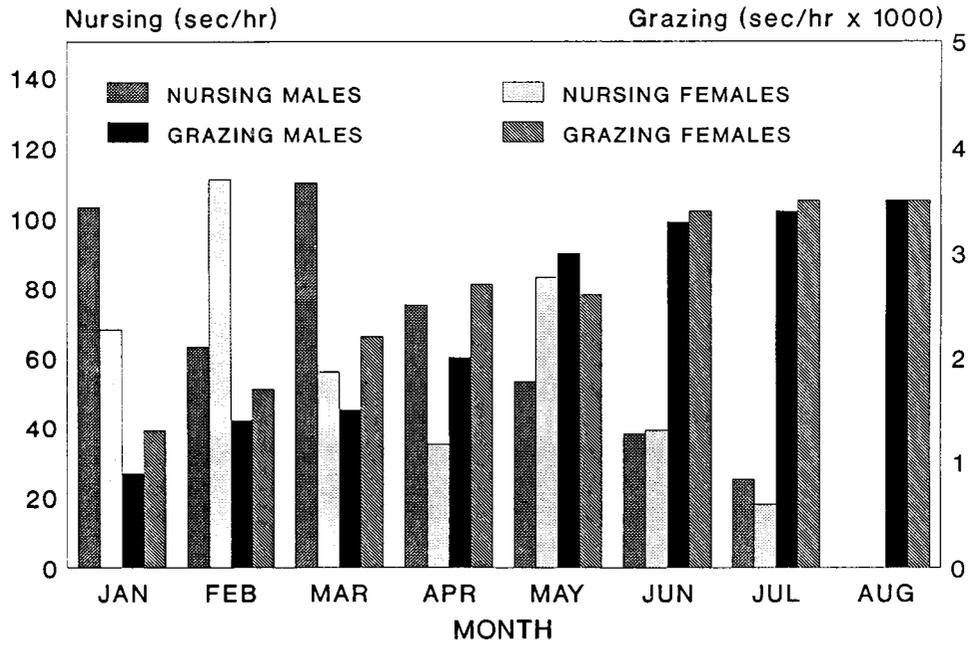


Fig. 1: Average diurnal hourly rate of nursing and grazing/mon by free-ranging male and female guanaco chulengos at Torres del Paine National Park, Chile.

Tasa horaria diurna promedio de actividad de chulengos machos y hembras en el Parque Nacional Torres del Paine, Chile.

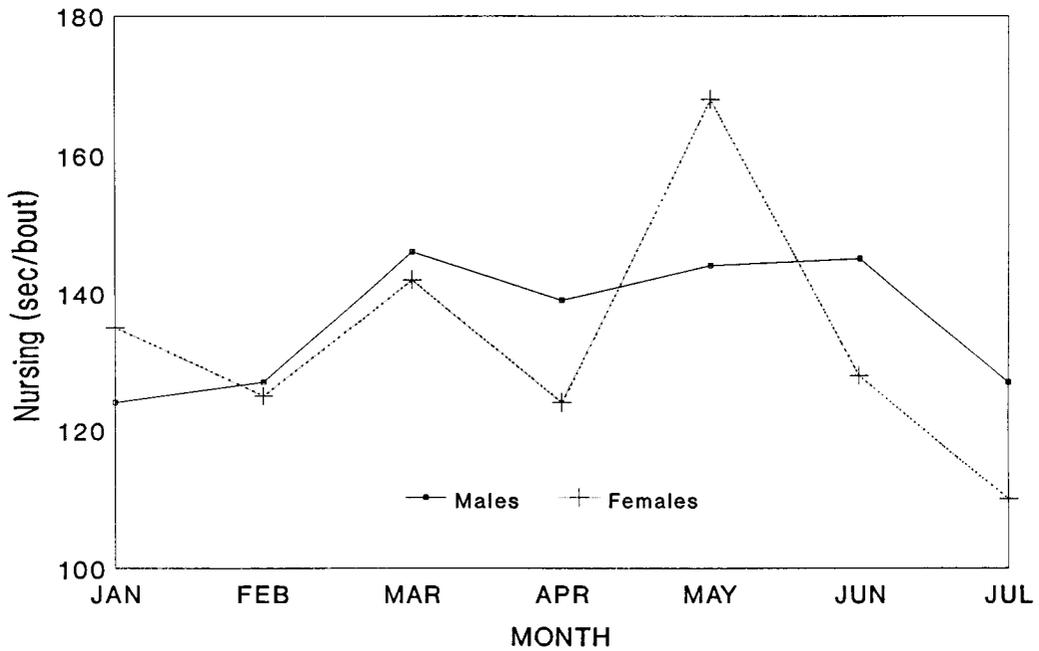


Fig. 2: Average duration of nursing/mon by free-ranging male and female guanaco chulengos at Torres del Paine National Park, Chile.

Duración promedio del amantamiento en chulengos hembras y machos en el Parque Nacional Torres del Paine, Chile.

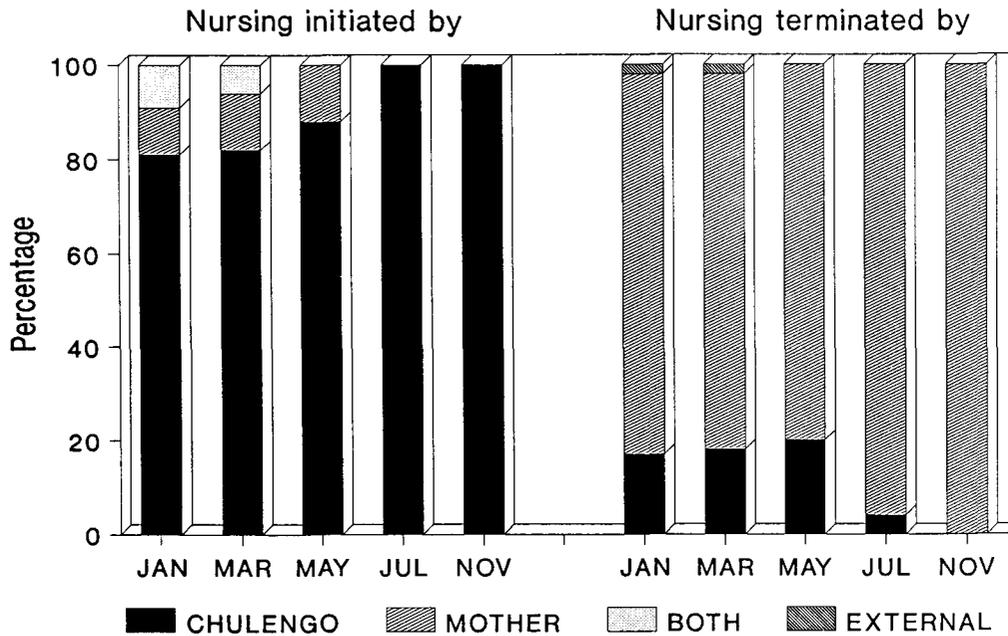


Fig. 3: Percentage of times guanaco chulengos and their mothers initiated and terminated nursings at Torres del Paine National Park, Chile.

Porcentaje de veces en que los chulengos y sus madres iniciaron y terminaron el amamantamiento.

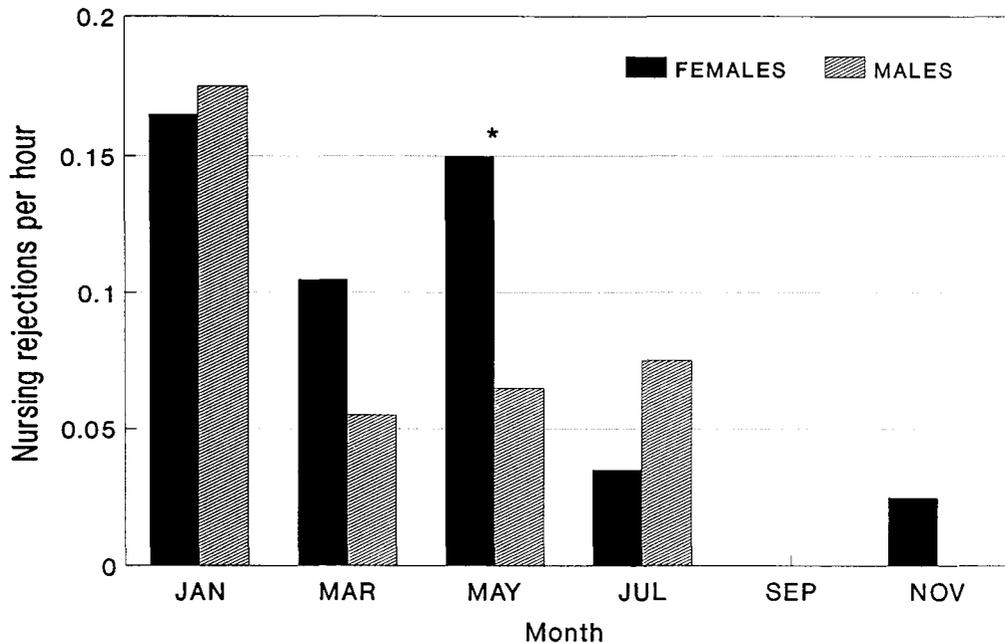


Fig. 4: Average diurnal hourly rate of nursing attempts rejected by mothers of male and female guanaco chulengos at Torres del Paine National Park, Chile.

Tasa horaria diurna promedio de intentos de amamantamiento de chulengos hembras y machos rechazados por las madres.

Chulengos spent nearly 50% of their time resting in early summer. The time spent resting decreased to 2.5% in winter, but then increased to an intermediate level the

following spring (Fig. 5). There were no differences between sexes in the amount of time spent resting ($P > 0.05$). Resting chulengos tended to lie next to other chu-

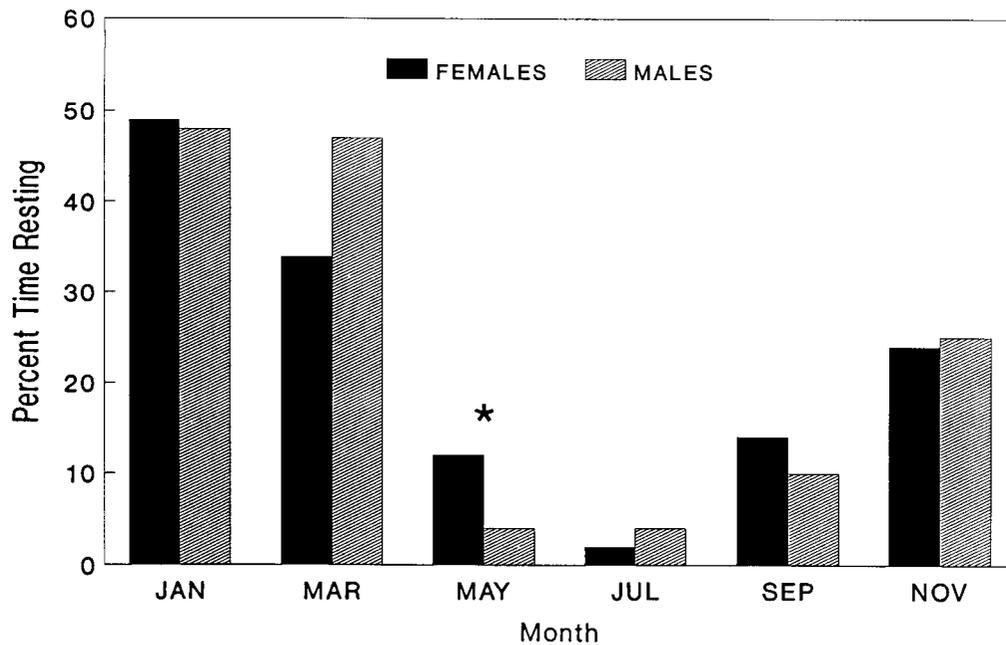


Fig. 5: Average percentage of diurnal time resting by free-ranging male and female guanaco chulengos at Torres del Paine National Park, Chile.

Porcentaje promedio de tiempo de descanso diurno por chulengos hembras y machos en el Parque Nacional Torres del Paine, Chile.

lengos during the day, but by their mothers at night.

Chulengos were the most active in mid-summer (January, $F = 4.69$, $P < 0.01$, $d.f. = 1,8$), when they spent 12% of their time walking, especially in association with exploring and investigating new and strange objects in their environment, such as unfamiliar guanacos, passing foxes, birds, etc., and moving towards their mother to nurse. Male chulengos were more active than females in January (15% vs. 9%, $F = 2.00$, $P < 0.05$, $d.f. = 1,8$). During the remainder of the year (March - November), the time spent walking varied from 2 to 5%, with no difference between sexes.

Chulengos spent significantly more time playing during the summer (January = 0.5 times/hr, 5% of the time, $F = 2.70$, $P < 0.05$, $d.f. = 1,8$), but exhibited negligible amounts of play in May, July, September, and November. Males spent significantly more time than females playing in January (males = 6%, females = 3%, $F = 2.37$, $P < 0.05$, $d.f. = 1,8$) and March (3% vs 0%, $F = 43.0$, $P < 0.01$, $d.f. = 1,8$). During the summer, chulengos played primarily between 1100 and

1300 hr (67%), followed by a second play period between 1600 and 1700 hr (15%). In fall and winter, all play was restricted to between 1300 and 1400 hr (100%).

Chulengos exhibited submissive behavior towards adult males throughout the year, with significant peaks in May (0.47/hr) and November (0.75/hr) ($F = 7.55$, $P < 0.01$, $d.f. = 1,8$) (Fig. 6). In March and May male chulengos exhibited a greater frequency of submissive crouches than females ($F = 3.67$, $P < 0.01$, $d.f. = 1,8$). Most subordinate behavior was in the form of submissive crouches (Franklin 1983, Wilson & Franklin 1985) in response to the adult male of the group: January 46%, March 44%, May 59%, July 80%, September 93%, and November 83%. Submissive interactions with the male in January and March were initiated by the chulengo (i.e. chulengos moved towards the male without him necessarily being aggressive). Towards the end of the chulengos first year (September and November), however, movements by the male within 50 m often caused chulengos to display submissive postures. During the summer and spring, the high rates of submission co-

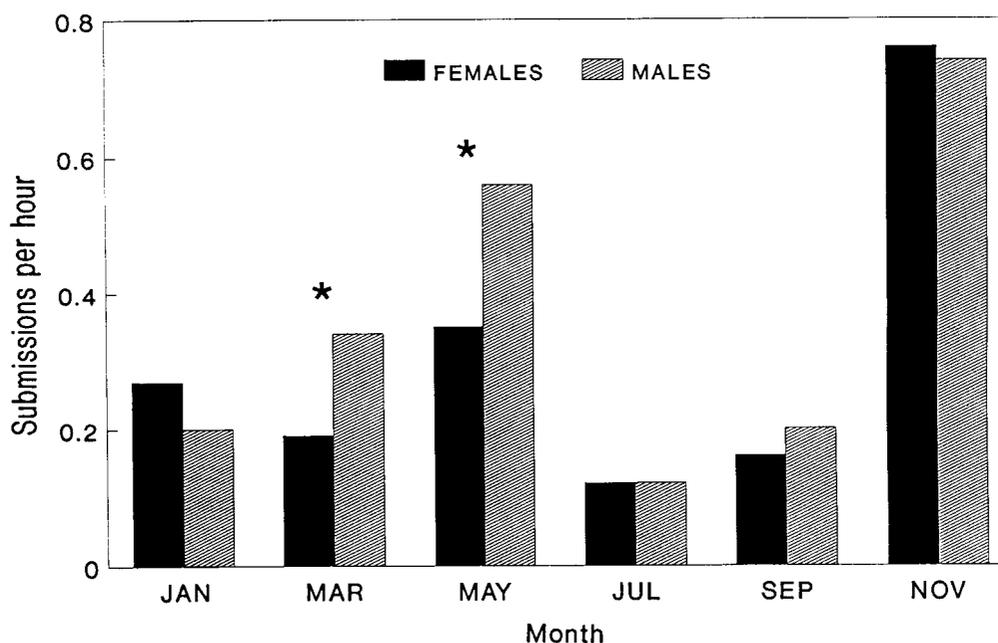


Fig. 6: Average diurnal hourly rate of submissive crouches by male and female guanaco chulengos at Torres del Paine National Park, Chile.

Tasa horaria diurna promedio de agachamientos de sometimiento por chulengos hembras y machos.

incided with peaks of Family Group activity, which occurred between 1100 -1200 hr (37% of submissions for those seasons) and 1400 -1500 hr (12%). In fall and winter, submissions occurred throughout the day, with a peak from 1300 - 1400 hr (32%).

November was a critical period for chulengos as they faced imminent expulsion by the adult male of the Family Group. The percentage of chulengos showing submissive behavior increased from 6%/hr to 70%/hr from week one to week three in November. The average duration of submissive crouches in November from week one to week three increased from 0.52 to 0.82 min/hr.

Chulengos were highly sensitive to the behavior and movements of the adult male during November. In the first week of November, 50% of the submissive crouches were in response to the male directly attacking chulengos and the other half were during his feeding or territorial defense activities. In the second week, 30% were in response to attacks on them by the male and the balance in response to the male walking, feeding, and interacting with other males. In the third week, 20% occurred from direct attacks, 21% from attacks to other chulengos in the

group, and 59% from other activities of the male. By the end of the month, 69% were full submissive crouches, i.e. tail in a full forward curl, head and neck lowered to the ground, and knees slightly bent (Franklin 1983). Most male chulengos were expelled by the first week in November, while female chulengos were expelled in the second half of November and the first week of December.

DISCUSSION

The movements and social changes which occurred during this study were similar to those described by Ortega (1985) and Ortega and Franklin (1995) for the same population, emphasizing the importance of birthing, expulsion, mating, and migration. The development of chulengo social behavior can best be understood in the context of the changes occurring in group structure and social behavior. The amount of time spent in different activities was also affected by the group's activity, but also changed in response to differing energetic demands related to the changing seasons and the transition

from nursing to grazing. Ultimately, these behaviors can be interpreted in terms of increasing the chulengo's probability of survival.

Most nursing occurred during the first few months, with the frequency of nursing decreasing with age (duration of nursing bouts, however, did not change). Chulengos started grazing during their first month, and relied almost exclusively on grazing by 8 months of age. Nursing may be of greater importance to males, because during some months male chulengos spent less time grazing, and more time nursing, playing, and exploring than females.

Nursing, because of its high energetic cost, also has an important influence on adult female behavior. Female guanacos must balance the energy invested in their chulengo with several factors. Energy expended in lactation is very high (Loudin and Kay 1984, Robbins and Robbins 1979, Sadleir 1980, Verme 1989) and nursing termination is one of the most direct ways females can limit the amount of energy invested in their young. The energy expended in milk production should be a balance between the minimum amount sufficient in raising a healthy chulengo and any added advantage in increased long-term fitness that might be accrued from more prolonged nursing. Mothers must also balance the tradeoff made between investment in the current offspring and any future young. Although it is uncertain what percentage of females have young during successive years, body condition has been shown to be important in determining successive pregnancies in many ungulates (Clutton-Brock and Guinness 1975). Since guanacos have a gestation period of 11.5 months, energy spent on the current offspring may also have immediate ramifications on the developing fetus.

Thus, a conflict exists between the chulengo and its mother, and it is manifested by nursing patterns. During the first months, mothers initiated some nursing bouts, but as chulengos grew older, chulengos were more often the initiators and mothers more often the terminators of nursing. Mothers, however, have greater control over this interaction. For example, during late fall, mothers rejected nursing attempts by female

chulengos more often than attempts by males, reflecting either a greater frequency of initiations by females or perhaps a greater investment in male chulengos.

Play is another important activity of chulengos. Play is often defined as behavior in which the young develop, practice, and maintain physical and mental abilities and social relations that will be used throughout life (Fagen 1981). Although no systematic observations of specific play behavior were made in this study, play appeared to consist of running, mock fighting/aggression, and mock copulation. Each of these behaviors has an important role in future adult behavior. Play behavior was most common during the summer and virtually nonexistent during the winter, reflecting the energetic costs of playing. Chulengos appeared to have more energy to expend in play during the summer, when they were regularly nursing; the long days provided more time, and the weather was more favorable. Chulengos have less time and energy for play during the winter, when they must obtain most of their energy from low-quality forage and must expend more energy in keeping warm. Energetic demands were also apparent in walking and resting behavior: chulengos walked and rested with the greatest frequency in summer and lowest frequency in winter. Male chulengos appeared to be more active than females, spending more time playing and walking than females during the summer.

The decrease in alarm behavior was probably related to increased recognition and habituation to their environment. Newborn chulengos are unable to discriminate between potentially dangerous objects or events.

Olfaction was probably related to the development of recognition of other guanacos, since it is one of the principal means of individual recognition in animals (Kaplan and Blussell 1974, Koford 1957). The highest frequency of olfaction occurred in January when the new-born chulengos were becoming integrated into the Family Group, and in March when Family Groups were breaking down into the large Mixed Groups for the winter. Recognition of the Family Group is probably important in maintaining group cohesion and in the formation of

Family Groups again in the spring (Franklin 1983). The March peak in olfaction, especially interactions between chulengo females and the adult male, may be important for individual recognition and the potential avoidance of inbreeding once the chulengos are adults and of breeding age.

Aggressive interactions between group members, common to all of the South American camelids (Franklin 1982, Koford 1957, Wilson and Franklin 1985), are often related to the maintenance of individual space and sometimes to food resources in the immediate vicinity. Aggression was highest during March, reflecting the development of new social relations resulting from the breakdown of family units and the formation of the larger Mixed Groups. The greater frequency of aggression received by female chulengos compared with males during March is more difficult to explain, but is likely to be a function of female chulengos more commonly approaching other adult guanacos.

Another reflection of aggression is the rate of submissions (Eibl-Eibesfeldt 1974, Franklin 1983), which occurred throughout the chulengos' stay in the Family Group. The submissive body position of chulengos is very similar to their nursing position (Franklin 1982), suggesting that it is a ritualized behavior, demonstrating to the adult male that it is still a young, nursing individual. Chulengos will often attempt to nurse from their mothers when the adult male approaches.

The increase in submissive behavior in May is related to the incorporation of more adult males in the mixed groups, and therefore, the higher probability of chulengos coming in contact with strange males, especially during periods of increased activity. Submissions were highest during November, in response to the direct aggressions of the adult male attempting to expel the chulengo from the group. During this period, the chulengos became much more sensitive to the adult male, increasing the rate and length of submissive crouches and responding to males from much longer distances than before. Submissive behavior is interpreted as an attempt by the chulengo to remain in the relative protection of the Family Group for as long as possible (see Franklin 1983). The mother will often attempt to defend her chulengo from the male, and sometimes will also accompany the chulengo once it has been expelled from the group, thereby prolonging the period of investment and care.

It is important to view the patterns of social behavioral development of chulengos in terms of seasonal activities of guanaco Family Group behavior (Fig. 7). During the summer, when chulengos are in Family Groups, social behaviors relating to the development of nursing, playing, olfaction, and alarm behavior are important. During the winter, when the chulengos are in mixed groups and the weather conditions are more demanding, there are more chances of interactions with strange guanacos and less time

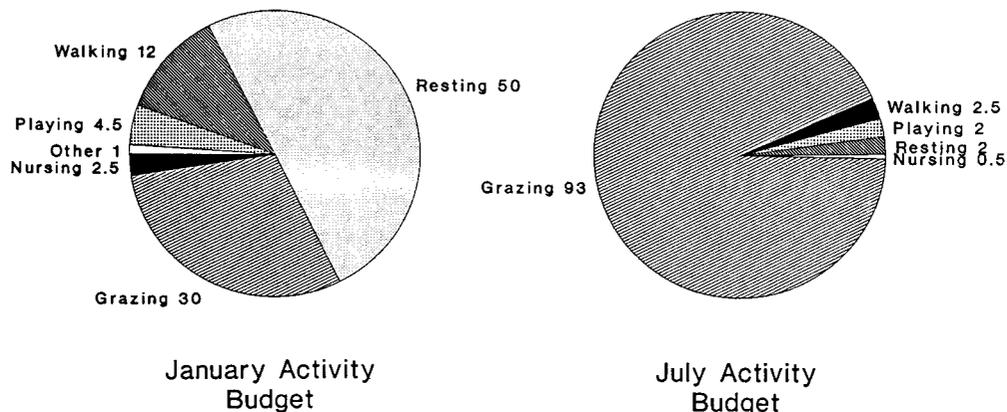


Fig. 7: Average percentage of time spent in different activities by guanaco chulengos.

Porcentaje promedio del tiempo gastado en diferentes actividades por chulengos.

and energy are available for activities other than feeding. As chulengos approach one year of age, their behaviors are dominated by the reformation of the Family Groups and by their eventual expulsion from the Family Group.

ACKNOWLEDGMENTS

We thank the administrative personnel of the Chilean Corporación Nacional Forestal (CONAF) in Torres del Paine National Park for their assistance with this investigation. The senior author expresses her appreciation to Morty Ortega, Paul Wilson and Mike Fritz for their advice, to Oscar Guineo and parents for their support, and to Julia Etchegaray (major advisor at the Chilean Catholic University) for her guidance. Field research was funded by a grant to William L. Franklin from the National Science Foundation (USA) Grant N° INT-8105084. This is Journal Paper N° J-15974 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project N° 2519.

LITERATURE CITED

- ALTMANN M (1960) The role of juvenile elk and moose in the social dynamics of their species. *Zoologica* 45: 35-39.
- ALTMANN J (1974) Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- CLUTTON-BROCK TH & FE GUINNES (1975) Behavior of the red deer (*Cervus elaphus* L.) at calving time. *Behavior* 55:286-299.
- EIBL-EIBESFELDT I (1974) *Etología*. Ediciones Omega, S.A. Barcelona, 643pp.
- ESTES RD & RK ESTES (1979) The birth and survival of wildebeest calves. *Zeitschrift Fur Tierpsychologie* 50:45-95.
- FAGEN R (1981) *Animal play behavior*. Oxford University Press.
- FRANKLIN WL (1982) Biology, ecology and relationship to man of the South American camelids. Pages 457-489 in M.A. Mares, and H.H. Genoways (eds.). *Mammalian biology in South America*. University of Pennsylvania and the Pymatuning Ecology Lab.
- FRANKLIN WL (1983) Contrasting socioecologies of South America's wild camelids: the vicuña and guanaco. Pages 573-629 in Eisenberg, J.F. and D. Kleiman (eds.) *Advances in the study of mammalian behavior*. American Society of Mammalogists, Spec. Pub. N° 7.
- FRANKLIN WL & MA FRITZ (1991) Sustained harvesting of the Patagonia guanaco: is it possible or too late? Pages 317-336 in K. Redford and J. Robinson (eds.). *Rational utilization of neotropical wildlife*. University of Chicago Press.
- GARAY G (1986) *Desarrollo del comportamiento social infantil del guanaco (Lama guanicoe)*. Tesis Licenciado en Ciencias Biológicas, Pontificia Universidad Católica de Chile.
- JOHNSON WE, WL FRANKLIN & JA IRIARTE (1990) The mammalian fauna of the northern Chilean Patagonia: a biogeographical dilemma. *Mammalia* 54: 457-469.
- JURGENSEN TE (1985) *Seasonal territoriality in a migratory guanaco population* MS Thesis. Iowa State University, Ames, IA.
- KAPLAN J & M BLUSSELL (1974) Olfactory recognition in the infant squirrel monkey. *Developmental Psychology* 7: 15-19.
- KOFORD CB (1957) The vicuña and the puna. *Ecological Monographs* 27:153-219.
- LOUDIN ASI & RNB KAY (1984) Lactational constraints of a seasonally breeding mammal: the red deer. *Symposia of the Zoological Society of London* 51: 233-252.
- ORTEGA IM (1985) *Social organization and ecology of a migratory guanaco population in southern Patagonia*. MS Thesis, Iowa State University, Ames, IA.
- ORTEGA IM & WL FRANKLIN (1988) Feeding habitat utilization and preference by guanaco male groups in the Chilean Patagonia. *Revista Chilena de Historia Natural* 61: 209-216.
- ORTEGA IM & WL FRANKLIN (1995) Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. *Revista Chilena de Historia Natural* 68: 489-500.
- PISANO E (1974) *Estudio ecológico de la región continental sur del área andino patagónica. II Contribución a la fitogeografía de la zona del Parque Nacional Torres del Paine*. *Anales del Instituto de la Patagonia* 5:59-104. (Punta Arenas, Chile).
- ROBBINS CT & BL ROBBINS (1979) Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *American Naturalist* 114:101-116.
- SADLEIR RMFS (1980) Milk yield of black-tailed deer. *Journal of Wildlife Management* 44:472-478.
- VERME LJ (1989) Maternal investment in white-tailed deer. *Journal of Mammalogy* 70:438-442.
- SAS INSTITUTE. 1989. *SAS/STAT user's guide*. 6.03 ed. SAS Institute, Inc. Cary, North Carolina.
- WILSON P & WL FRANKLIN (1985) Male group dynamics and inter-male aggression of guanacos in Southern Chile. *Zeitschrift Fur Tierpsychologie* 69:305-328.