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Maternal expenditure and the resolution of adult-offspring  
conflict in the South American guanaco

by

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A dissertation submitted to the graduate faculty  
in partial fulfillment of the requirements for the degree of  
DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

Major Professor: William L. Franklin

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**ABSTRACT**

I examined patterns of pre-/post-birth maternal energy expenditure in the polygynous guanaco, *Lama guanicoe*, in Torres del Paine National Park, Chile from November 1990 to December 1993. Because of presumed greater variance in reproductive success of males of polygynous species, theoreticians have hypothesized that greater parental energy investment in sons might improve their competitive abilities and lead to increased reproductive success. The period of parental care in guanacos is punctuated by an interval of intense parent/adult-offspring conflict. Adult males seasonally defend feeding territories and during spring become increasingly aggressive toward all juveniles and begin expelling them in October. In an apparent effort to appease territorial male aggression, juveniles display "submissive crouches" (SCs) when being attacked or closely approached by them. It is not known if more submissive animals remain in family groups longest before expulsion, or if they are able to avoid being expelled. Additionally, juvenile males appear to be expelled before juvenile females. Thus, juvenile males might be under greater selective pressure to be more submissive, especially if this strategy serves to reduce territorial male aggression and delays expulsion.

Contrary to our predictions concerning maternal energy expenditure, we found no apparent evidence of differential

energy expenditure on sons or daughters. Birth weight of males and females was similar, and suckling times of males and females were also not significantly different.

Submissive crouch frequency of juveniles that were expelled early, late, or not expelled increased with time in family groups before expulsion and were also significantly different from each other ( $P = 0.062$ ). There was a significant positive correlation between the frequency of territorial male aggression and submissive crouches. Juvenile males generally displayed more SCs/hr and for longer duration than juvenile females in almost all months/seasons. They did not remain in family groups longer than juvenile females, however. Juvenile males generally moved among more groups. The more groups that juvenile females moved among, however, the earlier they were expelled; this trend was not evident for juvenile males. Although juvenile males were generally expelled before juvenile females, the proportion of juvenile males and females that were expelled was not significantly different.



## CHAPTER 1. GENERAL INTRODUCTION

### Introduction

Understanding the evolution of parental care is of paramount importance in increasing our knowledge of mating systems, since many of the most prominent differences in the reproductive behavior of males and females are associated with their involvement in parental care (Clutton-Brock 1991).

Patterns of parental care in large, polygynous, dimorphic mammals demonstrate that sons garner more energy than daughters (Clutton-Brock 1991). Considerably less attention, however, has focused on patterns of parental care in polygynous monomorphic mammals. Because the number of studies addressing patterns of parental care in polygynous monomorphic mammals is limited, there exists no broad theoretical framework predicting how monomorphic parents should provision their offspring.

Because parents and offspring share only half of their genes, they should be in conflict over the amount of parental care that is provided (Trivers 1974). Trivers (1985) also stated that the degree of relatedness to future siblings influences the duration of conflict between parents and progeny. In species in which dominant breeding males are replaced every year or two, conflict between parents and young is hypothesized to last long. This conflict could also be

long and perhaps more intense in species in which dominant breeding males are not assured of paternity. To offset this conflict, Trivers (1974) suggested that offspring might be able to modify their parents' behavior in such a way as to shift it toward the offspring's optimum level of care.

The guanaco (*Lama guanicoe*) is an excellent species in which to test hypotheses regarding patterns of parental care and the resolution of parent-offspring conflict. Guanacos are highly social, polygynous, and monomorphic (Franklin 1983). Additionally, because adult females and offspring move among many groups, paternity between territorial males and offspring is uncertain. Territorial males begin forcefully and aggressively expelling juveniles from family groups when they are approximately 1 year old. In an apparent attempt to reduce territorial male aggression and delay or avoid expulsion, juveniles exhibit submissive crouches when being approached, observed, or attacked by territorial males. The submissive crouch is an obvious and exaggerated subordinate behavior in which juveniles lower their long necks toward the ground, raise their tails, and bend their knees as they remain stationary or move away from the territorial male.

The overall goal of this study is to understand patterns of energy expenditure by mothers on sons and daughters, and to determine if strategies used by juveniles during the period of conflict increase the period of parental care. Thus, my

objectives were to 1) measure potential differences in pre- and post-birth energy expenditure by mothers on sons and daughters, 2) compare the amount of energy expenditure among years and identify possible factors influencing these differences, 3) and to address the evolutionary and ecological significance of juvenile appeasement of territorial male aggression during the period of conflict and how it relates to the duration of parental care.

### **Dissertation Organization**

Chapter 1 of the dissertation includes a general introduction. Chapters 2 and 3 are papers prepared for publication in the journals of Behavioral Ecology and Animal Behaviour, respectively. Chapter 2 addresses patterns of maternal expenditure in guanacos. Chapter 3 addresses how juvenile guanacos decrease adult male aggression and potentially prolong the period of parental care. Chapter 4 includes the general discussion.

### **Literature Review**

*Parental Care.*--Although Williams (1966) was the first to appreciate the relevance of parental care to mating competition, it was Trivers (1972) who laid the foundation for modern thinking about the evolutionary consequences of parental care. Based upon the ideas of Darwin (1871), Bateman

(1948), and Fisher (1958), Trivers (1972) emphasized the need to consider all ways in which parents contributed to the fitness of their offspring. These ideas led Trivers (1972) to propose the term "parental investment", which he defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring."

Trivers and Willard (1973) subsequently hypothesized that natural selection would favor parental ability to adjust offspring sex ratio according to their ability to invest in each sex; females could provision sons and daughters differently, or produce more of one sex. Trivers and Willard (1973) also proposed that in species in which the variance in reproductive success was greater in males than females, additional investment would benefit sons more than daughters. Maynard-Smith (1980) later restated this idea by predicting that it is advantageous for parents to invest more in offspring of one sex if a greater than average amount of investment increased survival or fitness of that sex.

Biased investment in male offspring has been documented in large, polygynous, dimorphic mammals (Clutton-Brock et al. 1982, Kovacs and Lavigne 1986, Lee and Moss 1986, Trillmich 1986, Anderson and Fedak 1987, Wolff 1988, Festa-Bianchet 1989, LeBoeuf et al. 1989, Hogg et al. 1992, Bérubé et al.

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1996). Parental investment patterns in red deer, *Cervus elaphus*, (Clutton-Brock 1982) and northern elephant seals, *Mirounga angustirostris*, (LeBoeuf et al. 1989) seemingly conform to the predictions of Trivers and Willard (1973) and Maynard-Smith (1980). Adult male reproductive success of both species was more variable than that of females and was influenced in part by body size (Clutton-Brock et al. 1988, Leboeuf and Reiter 1988, Haley et al. 1994). Additionally, juvenile red deer males suffered greater mortality than females during the period of parental care (Clutton-Brock et al. 1982, 1985).

Because the terminology used in various studies has often been misleading and vague, Clutton-Brock (1991, pp 8-9) proposed definitions for parental care, parental expenditure, and parental investment: 1) Parental care-"Any form of parental behavior that appears likely to increase the fitness of a parent's offspring", 2) Parental expenditure-"The expenditure of parental resources (including time and energy) on parental care of one or more offspring", 3) Parental investment-"The extent to which parental care of individual offspring reduces the parent's residual reproductive value (RRV)", or future ability to successfully rear offspring.

*Parent-offspring conflict.*--Trivers (1974) also appears to have been the first to generate an evolutionary basis to explain the period of parent-offspring conflict. Trivers

(1974, 1985) proposed that kinship theory could explain the conflict between parents and progeny. In sexually reproducing species, parents and offspring are only 50% related on average, thus a conflict of interest is expected to occur between parents and young over the amount and duration of parental care.

Theoretical treatments of parent-offspring conflict in mammals have focused on the period of resource termination (Trivers 1974, 1985, MacNair and Parker 1978, Parker 1985, Tokuda and Seno 1994). Trivers (1974, 1985) proposed that because offspring are smaller and less experienced than parents, they should employ psychological tactics to "induce" parents to provide more care than they are selected to give. Although studies addressing parent-offspring conflict have shown that offspring appear to gain more resources from parents when they resort to certain behavioral tactics (Trivers 1985, Clutton-Brock 1991), the relative number of studies on mammals is limited.

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CHAPTER 2. MATERNAL EXPENDITURE IN THE POLYGYNOUS AND  
MONOMORPHIC SOUTH AMERICAN GUANACO: PREDICTABLE SEX-BIASED  
DIFFERENCES OR CHANCE?

A paper submitted to Behavioral Ecology and Sociobiology  
Ronald J. Sarno and William L. Franklin

**Summary.** We investigated patterns of pre-/post-birth maternal expenditure in the polygynous, monomorphic guanaco (Lama guanicoe) from 1990 to 1994. Because of their polygynous mating system, we hypothesized that maternal expenditure would be greater on sons than daughters. Differential maternal expenditure could occur by either providing more care to sons or producing sons when in good condition. Contrary to our hypothesis, we found no apparent evidence of differential maternal expenditure on sons or daughters. Birth weight of males and females was similar, and the birth sex ratio was not significantly different from 1:1. Although mothers rejected the suckling attempts of males significantly more often than females during fall and winter, suckling times of males and females were not significantly different for the year. Also, mothers with sons terminated suckling bouts in equal proportion as did mothers with daughters. Mean yearly capture weight (pre-birth maternal expenditure) was significantly negatively correlated with population size. Birth weight

decreased  $\approx 0.4$  kg with an increase of 500 animals. Mean annual suckling time was significantly different among years, as was the mean number of suckling attempts and rejected suckling attempts/hr throughout the year. There is a possible negative association between suckling behavior and population size, but more data are needed. In this guanaco population variance in maternal expenditure was greater among years than between sexes. This trend may also apply to other polygynous monomorphic/dimorphic ungulates that show relatively high levels of maternal reproductive effort.

*Key Words:* guanaco, *Lama guanicoe*, maternal expenditure, Chile.

Maternal expenditure (ME) (Clutton-Brock 1991, Hogg et al. 1992) in large ungulates has been elucidated principally for polygynous dimorphic species (Clutton Brock et al. 1982, Wolff 1988, Festa-Bianchet 1989, Hogg et al. 1992, Bérubé et al. 1996). Considerably less attention, however, has focused on ME in large polygynous monomorphic ungulates, and has been limited to wild and Przewalski horses (*Equus caballus*, *Equus przewalski*; Duncan et al. 1984, Berger 1986, Boyd 1988).

Because of monomorphism and assumed equal growth rates (and equal energetic demands) of juvenile males and females, greater expenditure on sons could suggest an evolutionary strategy adopted by mothers that would differentially benefit sons. Conversely, no differential ME on offspring could

suggest that these patterns are governed more by energetic demands on adult females rather than an evolutionary strategy adopted by adult females to benefit sons. If parents of polygynous monomorphic species expend more on offspring of one sex, such differences would occur before birth in the form of sex ratio adjustment or after birth as differential care to sons and daughters.

Trivers and Willard (1973) hypothesized that natural selection would favor parental ability to adjust offspring sex ratio according to the parents' ability to raise each sex; females could provision sons and daughters differently, or produce more of one sex. Regardless of the strategy females employ, they should do so contingent upon their own body condition. Trivers and Willard (1973) proposed that in species in which variance in male reproductive success was greater than that of females, additional ME would benefit sons more than daughters in terms of future reproductive success of offspring. This prediction assumes that 1) offspring condition at the end of the ME period is correlated with parental condition during ME, 2) offspring condition at the end of ME will continue into adulthood, and 3) slight advantages in body condition will differentially increase adult male reproductive success compared to that of females. Maynard-Smith (1980) later restated this idea by predicting that it is advantageous for parents to expend more energy on

offspring of one sex, if, for those individuals, a greater-than-average amount of energy increased survival or fitness, relative to the opposite sex.

Biased ME in male offspring has been documented in various large, polygynous, dimorphic mammals (Clutton-Brock et al. 1982, Kovacs and Lavigne 1986, Lee and Moss 1986, Trillmich 1986, Anderson and Fedak 1987, Wolff 1988; but see Green and Berger 1990, Festa-Bianchet 1989, LeBoeuf et al. 1989, Hogg et al. 1992, Bérubé et al. 1996). The investment patterns in red deer (Cervus elaphus, Clutton-Brock et al. 1982) and northern elephant seals (Mirounga angustirostris, LeBoeuf et al. 1989) seemingly conform to the predictions of Trivers and Willard (1973) and Maynard-Smith (1980). Adult male reproductive success of both species was more variable than that of females and was influenced in part by body size (Clutton-Brock et al. 1988, LeBoeuf and Reiter 1988, Haley et al. 1994). Furthermore, juvenile red deer males suffered greater mortality than females during the period of parental care (Clutton-Brock et al. 1982, 1985). Data for various polygynous dimorphic ungulates also demonstrate an overproduction of sons or daughters relative to adult female body condition, which seemingly support Trivers and Willard's (1973) hypothesis (Charnov 1982, Clutton-Brock et al. 1982, 1984, Clutton-Brock and Iason 1986, Rutberg 1986).

In polygynous monomorphic ungulates, how should parents

invest in their offspring? The models of Trivers and Willard (1973) and Maynard-Smith (1980) are also useful for generating hypotheses. Because of probable greater variance in male reproductive success of polygynous monomorphic ungulates, we hypothesized that sons should receive greater ME than daughters. Because males will be the more expensive sex to rear, mothers should produce sons when they are in relatively good condition and daughters when in relatively poor condition.

Sex-biased ME in monomorphic horses demonstrate that such patterns are not limited solely to polygynous dimorphic species. The data suggest that males gestate longer, suckle more often, and acquire more milk than females (Duncan et al. 1984, Berger 1986, Boyd 1988).

The guanaco (Lama guanicoe) could be a model species for testing predictions of maternal expenditure in a large, polygynous, monomorphic ungulate. Adult males seasonally defend food resources essential to females, thereby resulting in a resource-defense-polygyny mating system (Franklin 1983). Mean body weight and length of adult males and females are equal (Raedeke 1978). Besides larger canines, adult males possess no other secondary sexual characteristic that distinguishes them from adult females. Females produce one chulengo (offspring between birth and age 1) per year and offspring accompany their mothers until approximately 1 year

old, at which time adult territorial males begin forcefully expelling yearlings from the family group (Franklin 1983, Garay et al. 1995, Sarno unpublished data). Juvenile males suffer greater mortality during the period of parental care (W. Franklin unpublished data), and generally disperse before juvenile females (Franklin 1983, Garay et al. 1995, Sarno unpublished data). Additionally, only 10 to 20% of adult males presumably breed in any given year, while approximately 70% of adult females produce young each year. (W. Franklin, unpublished data).

The objectives of this study were to 1) measure potential differences in pre-and post-birth maternal expenditure on sons and daughters based upon chulengo birth weight, birth sex ratios, and suckling behavior, 2) address potential differences in post-natal maternal expenditure in relation to birth weight, and 3) compare the amount of maternal expenditure among years, and identify possible factors influencing these differences. Because of greater male mortality during the period of parental care, earlier dispersal, and presumed greater variance in adult male reproductive success, we hypothesized that male chulengos would receive greater maternal expenditure than females. We also predicted that heavier chulengos would suckle longer, and thus receive greater post-birth maternal expenditure than chulengos from the lighter weight classes, and that the level

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of maternal expenditure would vary among years.

### Methods

The study was conducted from 20 Nov 1990 to 1 March 1994 in Torres del Paine National Park (51°3'S, 72°55'W), an International Man and Biosphere reserve located in the eastern foothills of the Andean mountain range of southern Chile. The park encompasses 2,400 km<sup>2</sup> and provides almost undisturbed habitat for wildlife. The study area was a 40 km<sup>2</sup> "peninsula" ranging from 200-400 m in elevation bordered by large lakes to the south, north, and west and a sheep ranch to the east. The landscape was open with rolling hills, vegetation was rarely > 1 m high, and animals were easily observed. Grasses (Festuca gracillana, Anarthrophyllum patagonium) and shrubs (Mulinum spinosum, Senecio patagonicus, and Berberis buxifolia) dominated this pre-Andean steppe (Pisano 1974). Habituation of this protected population facilitated approach on foot to within 5 to 10 m of guanacos without their retreat.

We captured and marked newborn chulengos (Franklin and Johnson 1994) between 18 November and 10 December of 1990 to 1992. Approximately 84% of the captures occurred between 20 November and 3 December. We sexed, weighed, and tagged chulengos in both ears with individually numbered ear tags. We also collected blood and fitted most chulengos with radio-transmitters mounted on expandable collars (modified from Keister et al. 1988). We captured 99 chulengos in 1990, 100

in 1991, and 98 in 1992, or about 20% of each cohort.

We collected data from 0830-1800 during Spring (September-expulsion), Summer (December-February), and Fall (March-May), and from 1000-1600 during Winter (June-August). We observed all randomly located focal chulengos for 1 hr, and also collected data on other marked chulengos present in the group (see Altmann 1974 for a detailed explanation of focal subgroup sampling). We followed all marked chulengos from birth until they dispersed from family groups unaccompanied by their mothers, unless they emigrated from the "peninsula" study area (which was rare) or died. One to four investigators were in the field year-round, for a total of 4,020 hrs of observation.

We collected information on birth weight, birth sex ratio, suckling time, frequency of suckling attempts and rejections, number of rejected suckling attempts, and the number of suckling terminations by mothers with sons vs. mothers with daughters. Because we captured 98% of the chulengos at birth or within 1 day after birth, we used capture weight as an indicator of birth weight and pre-birth maternal expenditure. Because of the reduction in the frequency of suckling bouts by the end of Summer (February), we analyzed suckling data by months from November-February, and thereafter by the seasons Fall, Winter, and Spring. We considered a chulengo suckling when we observed it on the



teat. A suckling attempt was noted as such when a chulengo lowered its head, raised its tail, and approached the teat. We recorded a rejected suckling attempt when the mother 1) moved away from her chulengo while it was reaching for her teat, 2) lifted her leg in order to block access to her teat, 3) or spit at the chulengo as it approached. The chulengo terminated suckling by relinquishing the teat and walking away. Mothers terminated suckling bouts either by walking away from the suckling chulengo or by lifting a hind leg. If a chulengo paused while suckling, we subtracted that time from the total suckling time.

We tested for within year differences between males and females in birth weights, mean suckling time/hr, mean suckling bout duration, mean number of suckling attempts and rejected suckling attempts/hr, using Student's t-test, and analyzed among-year differences of these variables using standard ANOVA techniques. We used Chi-square analysis to test if 1) sons and daughters terminated suckling bouts equally, 2) mothers rejected suckling attempts based upon offspring sex, and 3) mothers terminated suckling bouts based upon offspring sex. We also examined the relationship between suckling behavior and chulengo birth weight using Pearson correlation. We related mean cohort birth weight with population size and climate (mean temperature and total precipitation) from 1987 to 1993 (Franklin unpublished data), and used standard Pearson

to 1993 and used Pearson correlation and standard regression techniques to analyze these relationships (SAS Institute, Inc., 1989).

We calculated sample size (N) for our suckling data based upon the number of marked animals observed during a given time period, not upon the number of observations for each animal. Because the individual was the unit of measure, we believe that our unweighted means approach best describes the means and variances of our variables.

## **Results**

### *Birth Weight and Sex Ratios*

Birth weights of males and females were not significantly different in 1990 ( $t = 0.59$ ,  $df = 95$ ,  $P = 0.56$ ), 1991 ( $t = 0.26$ ,  $df = 98$ ,  $P = 0.79$ ) or 1992 ( $t = 0.23$ ,  $df = 93$ ,  $P = 0.82$ ) (Table 1). Combining the data produced a significant difference among years ( $F = 4.35$ ,  $df = 2$ ,  $287$ ,  $P = 0.02$ ), but no year\*sex interaction ( $F = 0.22$ ,  $df = 3$ ,  $287$ ,  $P = 0.88$ ) (Table 1).

There was no difference in the sex ratio (males:females) of captured chulengos within years (1990 53:46; 1991 46:54; 1992 49:49;  $\chi^2 = 1.13$ ,  $df = 2$ ,  $P = 0.57$ ), nor was there an overall difference from unity (males 148:149 females;  $\chi^2 = 0.002$ ,  $df = 1$ ,  $P = 0.96$ ) among years.

### *Climate, Population Size, and Birth Weight*

There was no significant correlation between mean cohort

Table 1. Mean birth weight by chulengo sex and cohort from 1990-1992 in Torres del Paine National Park, Chile. See text for test statistics and P-values.

Year	Sex	N	Mean Birth Weight (Kg)			
			Weight	SE	Cohort	SE
1990	Males	52	12.7	0.2	12.6	0.18
	Females	46	12.5	0.3		
1991	Males	45	13.1	0.3	13.1	0.19
	Females	54	13.0	0.3		
1992	Males	47	12.4	0.3	12.3	0.17
	Females	49	12.2	0.2		

birth weight and temperature or precipitation in either Winter ( $\underline{r} = -0.02, -0.63, N = 7, \underline{p} = 0.97, 0.13$ ) or Spring ( $\underline{r} = 0.35, -0.39, n = 7, \underline{p} = 0.44, 0.39$ ) from 1987 to 1993. Mean cohort birth weight, however, was significantly negatively correlated with population size on the peninsula ( $r = -0.871, \underline{p} = 0.011, N = 7$ , Figure 1). The slope of the fitted regression line ( $y = 13.90 - 0.0008x$ ) suggests that for an increase in population size of 500 animals (throughout the range of observed population sizes), mean chulengo birth weight decreased by  $\approx 0.4$  kg.

#### Suckling Behavior

There were no significant differences between male and female chulengos in either mean suckling time/hr (unequal variance  $\underline{t} = 0.001, df = 245.8, \underline{p} = 0.999$ , Figure 2), mean suckling bout duration ( $\underline{t} = 0.86, df = 261, \underline{p} = 0.390$ ), mean number of suckling attempts/hr (unequal variance  $\underline{t} = 0.48, df = 216.7, \underline{p} = 0.631$ ), or mean number of rejected suckling attempts/hr (unequal variance  $\underline{t} = 0.59, df = 179.5, \underline{p} = 0.554$ ; Table 2) throughout the study.

In fall and winter male chulengos ( $\bar{x}_{fall} = 0.85, SE = 0.08, N = 94; \bar{x}_{winter} = 0.60, SE = 0.11, N = 75$ ) attempted to suckle significantly more often than females ( $\bar{x}_{fall} = 0.65, SE = 0.08, N = 80; \bar{x}_{winter} = 0.31, SE = 0.05, N = 96$ ; unequal variance  $\underline{t}_{fall} = 2.15, df = 154.7, \underline{p} = 0.033$ ; unequal variance  $\underline{t}_{winter} = 2.26, df = 135.6, \underline{p} = 0.026$ ). The mean number of rejected suckling

Figure 1. Regression of yearly mean guanaco birth weight against population size on the peninsula in Torres del Paine National Park, Chile from 1987-1993.



Figure 2. Monthly-seasonal mean suckling time/hr of male and female juvenile guanacos from the 1990-1992 cohorts in Torres del Paine National Park, Chile. Fall, winter, and spring occur from March through May, June through August, and September through November. Extending lines indicate standard error. Numbers above bars represent sample size for females and males, respectively.

## Chulengo Suckling

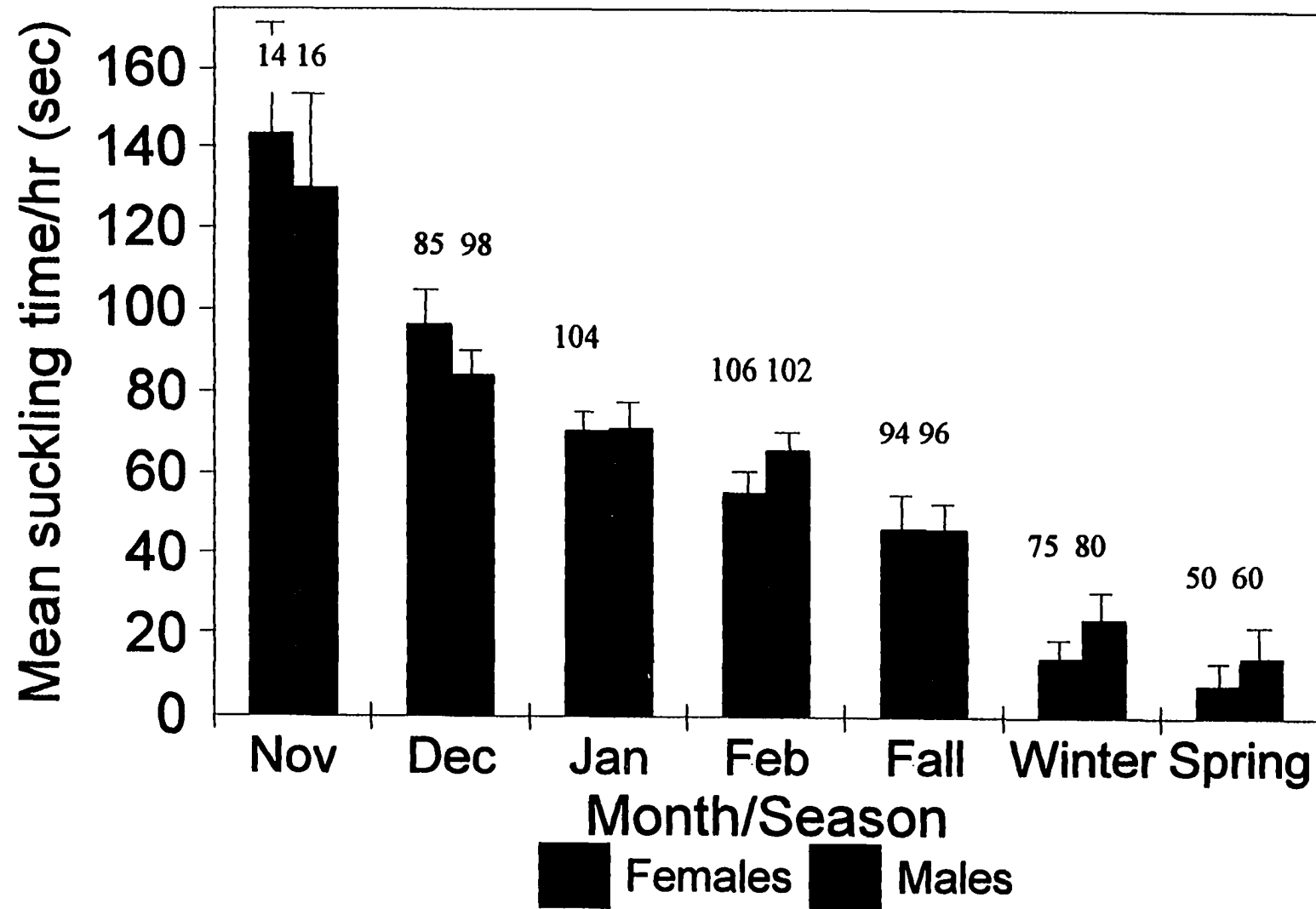




Table 2. Mean suckling time/hr, mean suckling bout duration, mean number of suckling attempts/hr, and mean number of rejected suckling attempts/hr of chulengos in Torres del Paine National Park, Chile from 1990-1992. See text for test statistic and P values.

<u>Mean Suckling Time (sec)</u>					
<u>Chulengo Sex</u>	<u>N</u>	<u>per/Hour</u>	<u>SE</u>	<u>per/Bout</u>	<u>SE</u>
Males	129	57.8	3.01	47.8	2.54
Females	134	57.8	4.00	44.7	2.42
<u>Nursing/Hour</u>					
		<u>Attempts</u>	<u>SE</u>	<u>Rejections</u>	<u>SE</u>
Males	129	1.00	0.70	0.39	0.03
Females	134	1.07	0.12	0.44	0.08

attempts/hr of males in fall ( $\bar{x} = 0.41$ ,  $SE = 0.66$ ,  $N = 94$ ) and winter ( $\bar{x} = 0.36$ ,  $SE = 0.09$ ,  $N = 75$ ) were also significantly higher than those of females ( $\bar{x}$  fall = 0.24,  $SE = 0.03$ ,  $N = 96$ ;  $\bar{x}$  winter = 0.14,  $SE = 0.04$ ,  $N = 80$ ; unequal variance  $t_{fall} = 2.38$ ,  $df = 142$ ,  $P = 0.019$ ; unequal variance  $t_{winter} = 2.10$ ,  $df = 96.9$ ,  $P = 0.038$ , Figure 3). Although mothers terminated the greatest number of suckling bouts (67%), there was no difference between mothers with sons vs mothers with daughters ( $\chi^2 = 2.74$ ,  $df = 1$ ,  $P = 0.98$ ).

#### *Yearly Comparisons*

Mean suckling time/hr throughout the year differed significantly among cohorts ( $F = 3.18$ ,  $df = 2$ , 1058,  $P = 0.042$ ), but mean suckling bout duration throughout the year did not ( $F = 2.30$ ,  $df = 2$ , 1058,  $P = 0.101$ , Figure 4) differ significantly among cohorts. There were significant differences among cohorts in the mean number of suckling attempts/hr ( $F = 3.05$ ,  $df = 2$ , 1058,  $P = 0.048$ ), and mean number of rejected suckling attempts/hr ( $F = 3.28$ ,  $df = 2$ , 1058,  $P = 0.038$ , Figure 5).

There were also differences in the proportion of chulengo suckling attempts rejected by mothers among cohorts (1990=43%, 1991=47%, 1992=32%;  $\chi^2 = 48.4$ ,  $df = 2$ ,  $P < 0.0001$ ). Finally, the number of suckling bouts that mothers terminated also differed significantly among cohorts (1990=63%, 1991=67%, 1992=72%;  $\chi^2 = 11.0$ ,  $df = 2$ ,  $P = 0.004$ ).

Figure 3. Monthly-seasonal mean number of suckling attempts and rejected suckling attempts/hr of male and female juvenile guanacos from the 1990-1992 cohorts in Torres del Paine National Park, Chile. Fall, winter, and spring occur from March through May, June through August, and September through November. Extending lines indicate standard error. Numbers above bars represent sample size for females and males, respectively.

# Suckling Attempts and Rejections

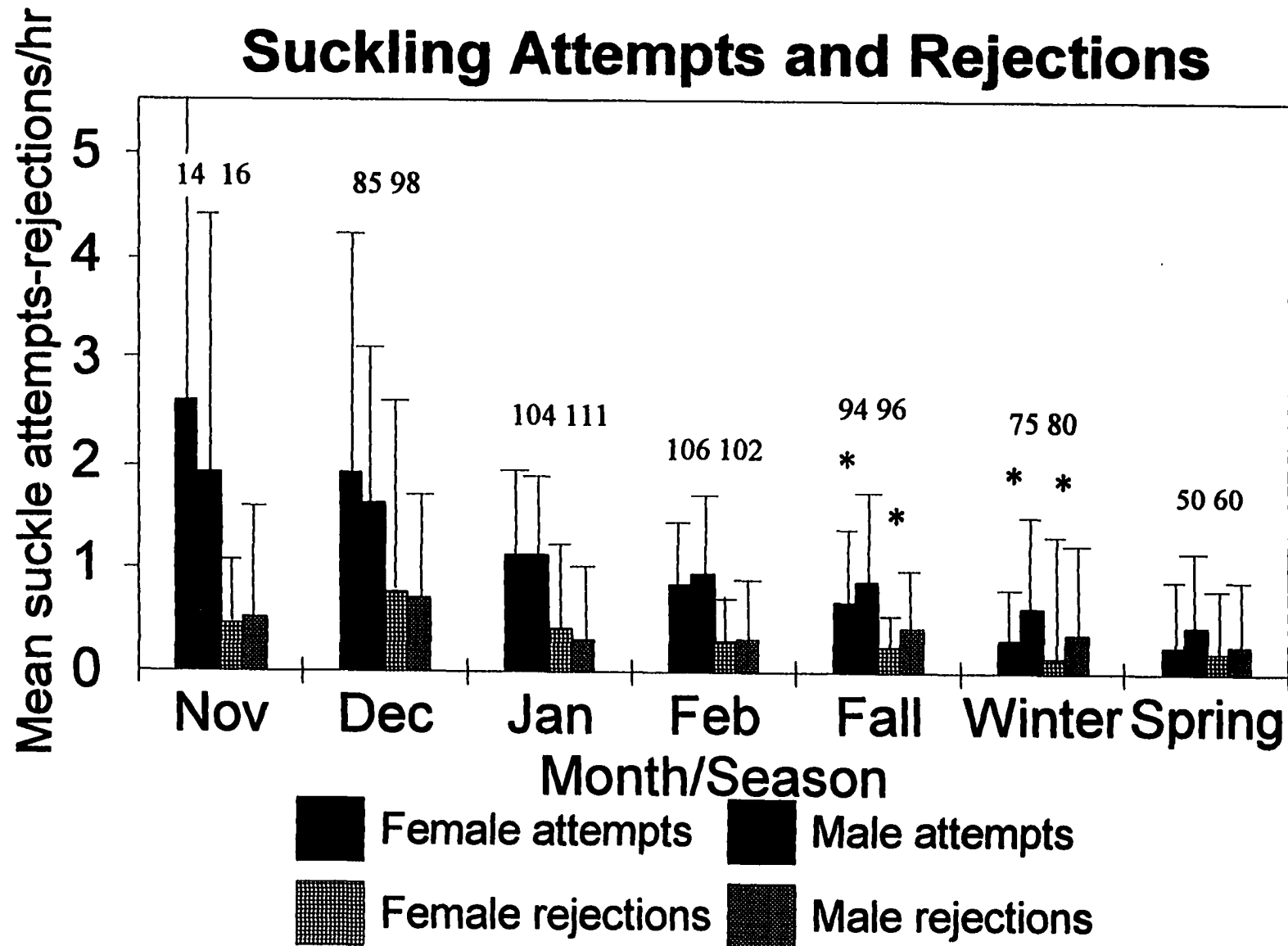


Figure 4. Mean suckling time/hr and mean suckling bout duration of juvenile guanacos on a yearly basis for the 1990-1992 cohorts (n = 259) in Torres del Paine National Park, Chile. Differences among cohorts are significant (see text for test statistic and P values). Extending lines indicate standard error.

## Suckling Duration

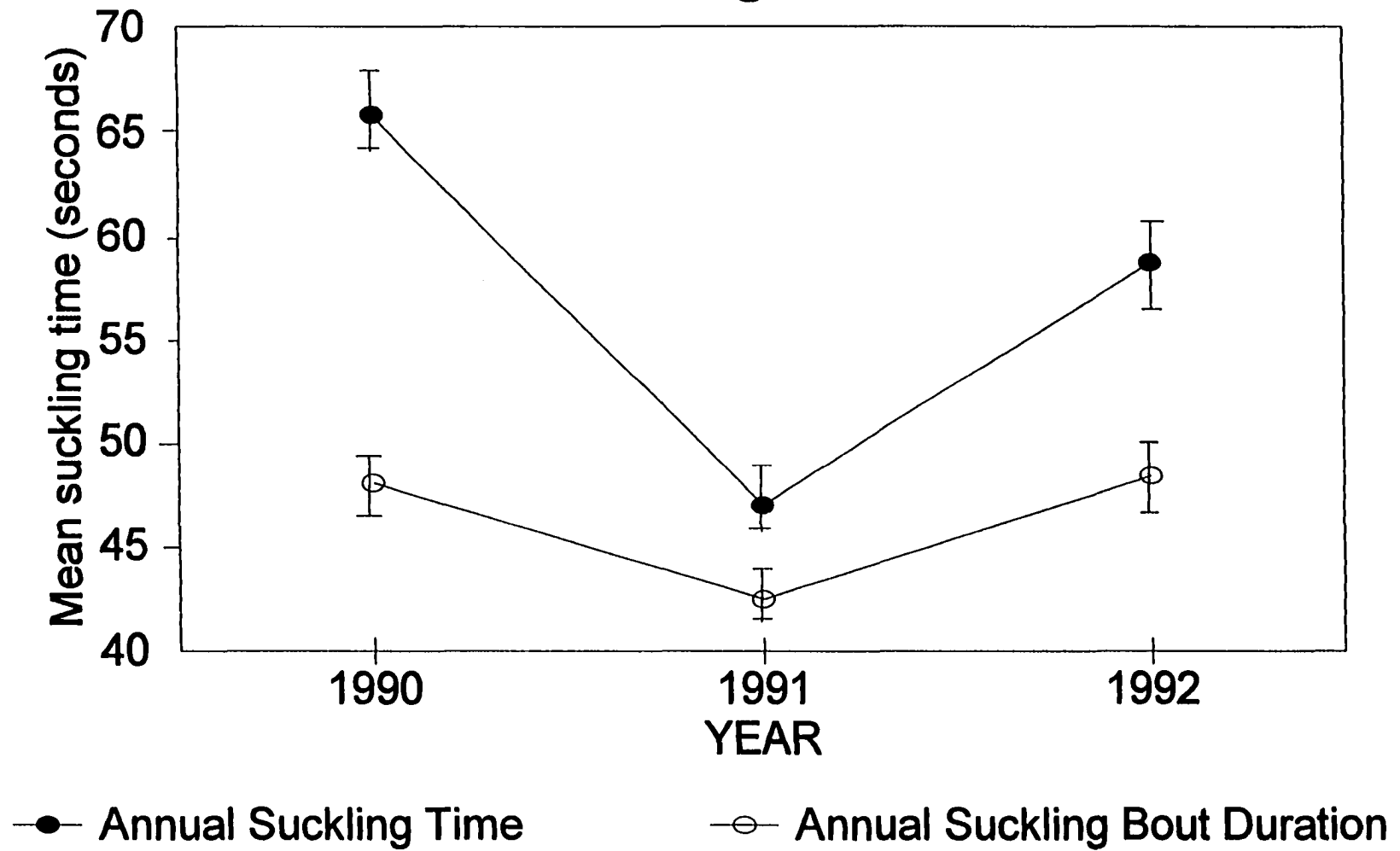
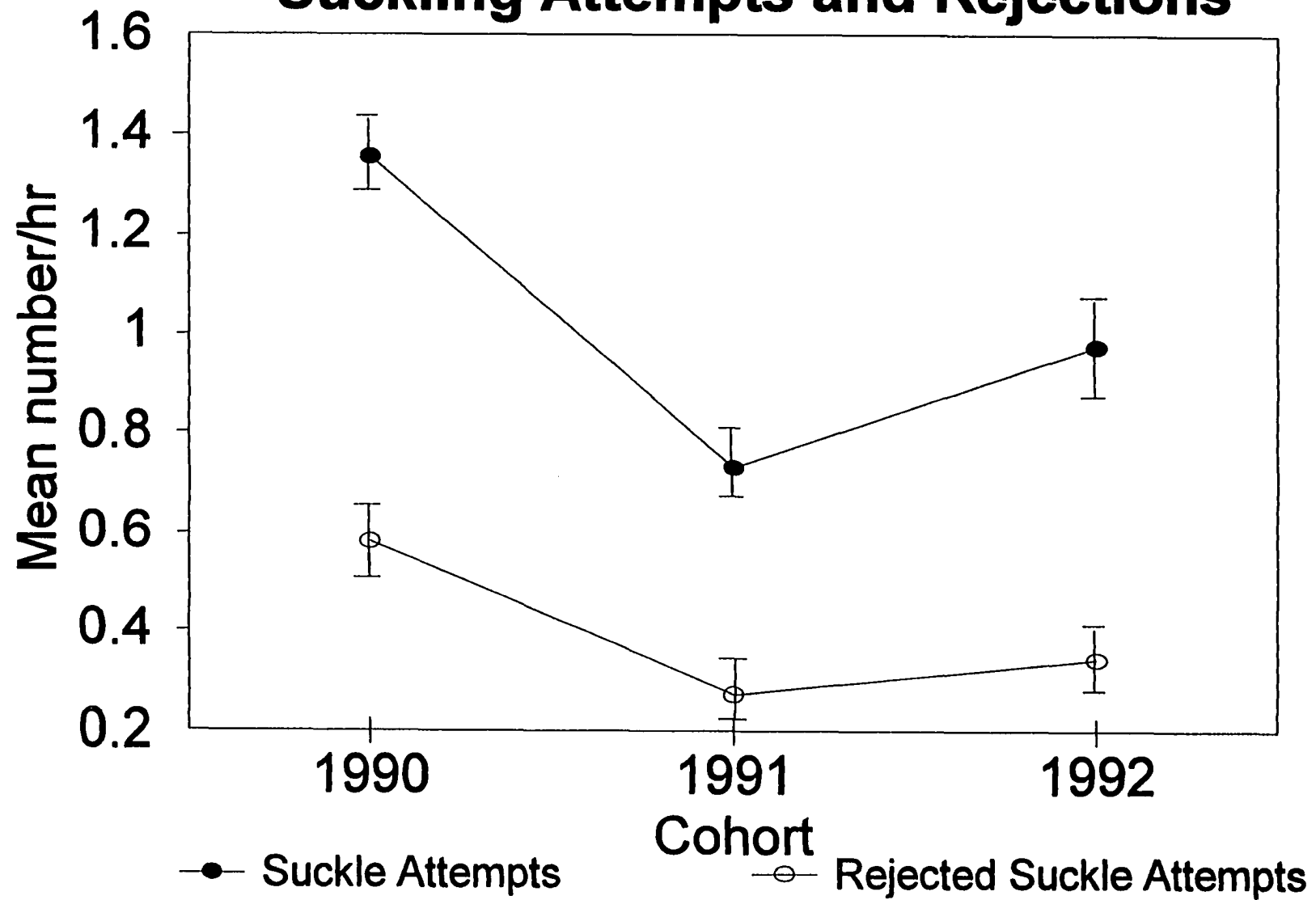


Figure 5. Mean number of suckling attempts and rejected suckling attempts/hr of juvenile guanacos on a yearly basis for the 1990-1992 cohorts (N = 259) in Torres del Paine National Park, Chile. Differences among cohorts are significant (see text for test statistic and P values). Extending lines indicate standard error.

## Suckling Attempts and Rejections





## Birth Weight

There was no apparent relationship between chulengo suckling behavior and birth weight. There was a significant negative correlation between mean suckling time/hr and birth weight ( $\underline{r} = -0.169$ ,  $N = 224$ ,  $\underline{P} = 0.021$ ). Because of the low  $r$  - value, however, we do not believe that this relationship is biologically meaningful. Additionally, there was no significant correlation between the mean number of suckling attempts/hr and birth weight ( $\underline{r} = -0.096$ ,  $N = 224$ ,  $\underline{P} = 0.150$ ), nor the mean number of rejected suckling attempts/hr and birth weight ( $\underline{r} = -0.011$ ,  $N = 224$ ,  $\underline{P} = 0.090$ ).

## Discussion

### *Pre-Birth ME And Sex Ratio*

There appears to be no differential pre-birth maternal expenditure on sons or daughters because of the equal birth weights of male and female chulengos. This is not surprising because of adult size monomorphism. We suspected that growth rates of males and females were equal before birth, and that one sex would not be born heavier than the other.

There was also no evidence of a significantly skewed birth sex ratio. Behl (1992), however, reported slightly more male (51.4%) than female (48.6%) chulengos born from 1987-1991 ( $N = 344$ ) for the same population. Biased birth sex ratios have also not been reported from multi-year studies of dimorphic red deer (Clutton-Brock et al. 1982), bison (Bison

bison) (Green and Rothstein 1991), or monomorphic horses (Berger 1986).

Trivers and Willard (1973) hypothesized that adult females should produce more sons when in good condition. From 1987 to 1993 population size on the peninsula generally increased each year. Because mean chulengo birth weight was significantly negatively correlated with population size on the peninsula, we assume that female body condition deteriorated as population size increased. Between 1987 and 1993 the general trend should have been the production of more females; we observed the production of more males (277:268). Because we do not have data on the condition of individual adult females it is difficult to interpret these data in reference to Trivers and Willard's (1973) hypothesis. Long-term studies which assess the body condition of known individuals are needed to better test Trivers and Willard's (1973) hypothesis. Perhaps in monomorphic polygynous species in which sons do not appear to be more expensive to raise than daughters, one might postulate the equal production of sons and daughters regardless of adult female condition.

We were unable to determine sex ratio at conception. Gestation lasts about 11.5 months (Franklin 1983), and body condition at conception could influence the primary sex ratio. It is possible that one sex could have suffered higher in-utero mortality. It is also possible that the duration of the

study was too short to observe significant differences in the sex ratio of chulengos or that the presumed body condition of females was not different enough among years to produce biased birth sex ratios.

There is some evidence that mammalian sex ratios can be skewed in relation to maternal condition. Clutton-Brock et al. (1982, 1984) observed that four-year-old primiparous red deer females, and dominant females, presumably in the best condition, produced more costly sons. Rutberg (1986) reported that non-lactating female bison carried significantly more male fetuses than lactating females. These data suggest that non-lactating cows were in better condition than lactating cows and produced more male calves.

Conversely, Verme (1969) reported that female white-tailed deer (Odocoileus virginianus) on the highest nutritional plane produced significantly more females, while Robinette (1973) and Skogland (1986) reported similar but non-significant trends in mule deer (Odocoileus hemionus) and reindeer (Rangifer tarandus tarandus), respectively. These results seemingly oppose Trivers and Willards' (1973) predictions, because of the greater production of females. This bias is potentially explained, however, by the varying costs and benefits of producing sons and daughters (Clutton-Brock and Iason 1986).

The Trivers and Willard (1973) hypothesis may provide

insight into the lack of consistent trends in skewed birth sex ratios. Body condition is probably a function of many components, including age, nutrition, population size (which in turn influences competitive interactions, dominance rank, and food quantity), climate, and vegetation quality.

Determining how these factors jointly influence body condition is likely very difficult for wild free-ranging ungulates.

Some factors undoubtedly vary more than others annually, thus influencing female condition and potentially offspring sex.

Variation in the overproduction of one sex might be expected because of continuously changing environmental and social conditions. Clutton-Brock and Iason (1986) stated, however, that several mechanisms may affect birth sex ratio, and all are not likely to be adaptive.

#### *Suckling Behavior*

Because of greater juvenile male mortality during the period of parental care, earlier juvenile male dispersal, and probable greater variance in adult male reproductive success, we hypothesized biased maternal expenditure on sons. There is no obvious differential post-birth maternal expenditure, because one sex does not appear to garner significantly more milk than the other. Garay et al. (1995) in a preliminary study with a much smaller sample size observed a similar trend.

It is puzzling that the number of suckling attempts by

male chulengos in fall and winter was significantly higher than that of females, but equal to that of females in spring. If one sex was apparently more costly to rear than the other because of differential growth rates for example, then differences in suckling behavior should have emerged at some point and continued throughout the year. Growth rates of male and female domestic alpaca (Lama pacos) crias, however, appear to be equal (Leon et al. 1989), and we assumed that guanaco post-natal growth rates were also equal. Aside from the enigmatic seasonal differences between males and females in the frequency of suckling attempts/hr, and hence rejected suckling attempts/hr, our hypothesis is not supported by the results.

Although male and female suckling times were not statistically different at our chosen alpha-level (0.05), possibly resulting from large variance in our suckling data, they could be *biologically* meaningful. Contrary to our hypothesis, daughters could have received substantially more energy than sons early in life. For example, the minimum mean difference in average suckling time/hr between chulengo females and males during December of any year was 5 seconds. Multiplying this value by 18 hrs for 31 days shows that the average female chulengo suckled  $\approx$  46.5 minutes longer than the average male during December, which equals almost 3 additional days of energy acquisition. Additionally, Garay et al. (1995)

reported that female chulengos suckled longer than males early in life, while the rate of suckling attempts was equal.

#### *Weight Class and Yearly Variation*

The non-significant relationship between chulengo birth weight and mean suckling time/hr, mean number of suckling attempts/hr, and mean number of rejected suckling attempts/hr do not support our hypothesis. We predicted that heavier chulengos should have greater energetic requirements than lighter chulengos, and that we would have observed a positive relationship between chulengo birth weight and mean suckling time, mean number of suckling attempts/hr, and/or mean number of rejected suckling attempts/hr.

We were surprised that the 1991 cohort (highest mean birth weight) exhibited the lowest mean annual suckling time/hr. We inferred that higher mean birth weight indicated relatively better adult female body condition. In support of this, the winter of 1991 was the mildest during the study. Pollard et al. (1993) reported that alpaca mothers in good condition provided sufficient energy for their crias to grow well, while mothers in poor condition raised offspring with poor growth rates. These data on alpacas suggest that adult female guanacos in good condition produce higher quality and/or more milk. Better quality milk would be more nutritious and potentially satiate offspring sooner than lower quality milk. Additionally, chulengos suckling from mothers

in good condition may receive more milk per unit suckling time than they would from mothers in poor condition. More milk in the mammary gland creates higher internal pressure, and offspring generally receive more milk per unit suckling time (Heald 1985). Additionally, high rates of milk removal stimulate greater milk production (G. Lindberg, pers. comm., Dept. Animal Science Iowa State Univ.). Thus it seems plausible that better and/or more milk might reduce suckling time by chulengos, and could explain the lower mean suckling time and mean number of suckling attempts/hr of chulengos born in 1991. There appears to be a positive relationship between mean suckling duration and number of suckling attempts/hr, but more data are needed to test this idea.

The number of rejected suckling attempts of male and female chulengos was not significantly different among cohorts. Mothers terminated the greatest proportion of suckling bouts for chulengos born in 1992, suggesting that adult females were in relatively poorer condition. Furthermore, the winter of 1992 was the most severe during the study. Perhaps nursing termination is more indicative of adult female body condition because it suggests decreased milk availability.

#### *Alternative Explanations*

Our data do not support the models of ME proposed by Trivers and Willard (1973) and Maynard-Smith (1980). In fact,

there are numerous studies of polygynous dimorphic species of mammals in which it appears that sons and daughters have received equal amounts of energy (Robins and Moen 1975, Mueller and Sadleir 1980, Gauthier and Barrette 1985, Carl and Robbins 1988, Byers and Moodie 1990). Byers and Moodie (1990) proposed that what limits differential ME in ungulates is the level of reproductive effort (offspring birth weight<sup>0.75</sup>/maternal weight<sup>0.75</sup>). Byers and Moodie (1990) stated that the amount of energy that mothers must provide to support rapid offspring growth rates, limits any extra provisioning of sons. Although a species may show adult size dimorphism, young males may be prevented from evolving higher growth rates during the period of parental care if mothers are already providing the maximum amount of energy possible.

#### *Factors Influencing Maternal Expenditure*

Variation in chulengo birth weight appears linked to population size. Although climate (e.g., Albon et al. 1983) has also been shown to influence offspring birth weight, it did not appear to influence chulengo birth weight in our study population. One of the likely social consequences of increased population size was more intense feeding competition. Individuals probably garnered less energy, and as a result, females produced lighter offspring. Effects of population density on growth, fecundity, birth weight, suckling time, and survival have been demonstrated in other



populations of mammals (Klein 1968, Caughley 1970, Geist 1971, Grubb 1974, Sinclair 1977, Clutton-Brock et al. 1982, Skogland 1984, Bérubé et al. 1996).

In certain situations, proximate causes such as climate and population density might rival the importance of the evolutionary consequences (i.e. intensity of mating competition and sexual selection) (Williams 1966) , or potential ultimate causes, governing differential pre-/post-birth ME on sons and daughters.

We conclude that adult female guanacos expend equal amounts of energy on sons and daughters, because of similar birth weights and suckling behavior. Our results support Byers and Moodies' (1990) hypothesis of maternal reproductive effort ( $\text{birth wt}^{0.75}/\text{maternal wt}^{0.75}$ ), because our calculated level (0.202) of reproductive effort for guanacos falls within the range of those species showing no differential maternal expenditure on offspring (Byers and Moodie 1990). For guanacos, as well as possibly other monomorphic-dimorphic polygynous mammals, we propose that differences in maternal expenditure will be greater among years than between sexes. In this population, a mothers' ability to supply pre-natal energy to her offspring seems related to population size. There is a possible negative relationship between suckling time and population size, but more data are needed. We suggest that increased understanding of patterns of maternal

expenditure, and other questions, falling under the rubric of parental care will only come with multi-year studies. Variation in patterns cannot be observed within one season or one year. In some populations of mammals, environmental conditions may influence patterns of maternal expenditure more than hypothesized ultimate evolutionary causes.

Although the models of Trivers and Willard (1973) and Maynard-Smith (1980) were very influential and sparked much empirical work, they have not been supported in various studies of polygynous ungulates. Perhaps the theoretical basis of these predictions needs modification. Even in studies which seemingly support these hypotheses, the ultimate causes of differential ME on offspring are not clear.

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CHAPTER 3. DO JUVENILE GUANACOS REDUCE ADULT AGGRESSION  
AND EXTEND THE PERIOD OF PARENTAL CARE?

A paper to be submitted to *Animal Behaviour*

Ronald J. Sarno, William L. Franklin, and Hal E. Stern

**Abstract.** We examined adult-offspring conflict in the guanaco, *Lama guanicoe*, in Torres del Paine National Park, Chile, from November 1990 to January 1994. The period of parental care in guanacos is punctuated by an interval of intense adult-offspring conflict. Adult males seasonally defend feeding territories and during spring become increasingly aggressive toward all juveniles and begin expelling them from family groups in October. In an apparent effort to appease territorial male aggression, juveniles display "submissive crouches" SCs when being attacked or closely approached by them. Juvenile males appear to be expelled before juvenile females, thus they might be under greater selective pressure to be more submissive, especially if this strategy serves to reduce territorial male aggression and delay expulsion.

Submissive crouch frequency of juveniles that were expelled early, late, or not expelled was different ( $P = 0.062$ ), and increased with time in family groups before expulsion. There was a significant positive correlation between the frequency of territorial male aggression and



juvenile submissive crouch rate. Neither the mean number of aggressive interactions/hr, nor the mean number of SCs/hr were significantly correlated with expulsion date. Juvenile males generally displayed more submissive crouches/hr and for longer duration than juvenile females in almost all months-seasons. Juvenile males also moved among more groups than juvenile females. The more groups that juvenile females moved among, however, the earlier they were expelled; this trend was not evident for juvenile males. Although juvenile males were generally expelled before juvenile females, the proportion of juvenile males and females that were expelled was not significantly different.

The period of parental care in mammals can be viewed as a contest between parent(s) and offspring. Parents have presumably been molded by natural selection to invest in each offspring so as to maximize the number of young that each produces throughout its lifetime. Offspring, however, should not be viewed simply as passive vessels into which parents pour resources, but can also be viewed as having evolved to extract more care from parents than they are selected to give (Trivers 1974, 1985). How can offspring possibly compete with parents for resources? They are smaller and less experienced. Given this competitive disadvantage, offspring should employ behavioral tactics to elicit more parental care than parents

are selected to give. It is not surprising, therefore, that conflict arises between parents and offspring due to differences in the way each has presumably evolved to maximize their fitness.

Trivers (1985) proposed that the degree of relatedness to future siblings affects the duration of parent-offspring conflict. In species in which breeding males are replaced every year or two, most siblings will be half siblings, and the period of conflict is expected to last longer and perhaps be more intense than in situations in which breeding males have longer tenure. This conflict should also be long and intense in species in which dominant breeding males are not assured of paternity. Under these conditions, can juveniles possibly diminish this conflict between themselves and parent(s) and/or adults? This could be critical in influencing the period of parental care, because adult aggression appears to be a proximate factor in terminating the period of parental care in various species of mammals (Dobson 1982, Wolff 1993, Wahlstrom 1994, McDonough 1994). Apparently no one has addressed if juveniles of these species have evolved mechanisms to deter adult aggression.

The social system of the South American guanaco (Lama guanicoe) has favored the evolution of extreme juvenile submissive behavior to decrease adult male aggression and to prolong the period of parental care. Guanacos are highly

social, monomorphic, and exhibit a resource-defense-polygyny mating system (Franklin 1983). As migrating animals arrive on the summer range in early spring (September), adult females and their young from the previous birth season join territorial males in the formation of family groups (a generic term in the sense that not all members are necessarily related). Chulengos (guanacos < 1 year old) are born in November and December, and family groups remain together from September to March (Franklin 1983, Ortega and Franklin 1995). Family groups begin dissolving in March and April, and all animals congregate in large mixed groups during the winter (June through August). Family group composition changes as adult females and juveniles (chulengos and yearlings- $\geq 1$  and < 2 years old) move among groups (Jurgensen 1985).

As spring progresses, adult territorial males become increasingly aggressive toward all chulengos from the previous birth season and begin expelling them from family groups in October (Franklin 1983). In an apparent effort to deter this aggression and delay expulsion, juveniles frequently display "submissive crouches" (SCs) when being approached, observed, or attacked by the territorial male. The submissive crouch is an obvious and exaggerated subordinate behavior in which juveniles lower their long necks toward the ground, raise their tails, and bend their knees as they move away from the territorial male. Juveniles also display "forced submissive

crouches" (FSCs see Franklin 1979). FSCs occur when the territorial male is away from the group feeding or interacting with another animal. Juveniles exhibit the same body position as a SC, but display them while approaching the territorial male up to 0.5 m.

Because of the assumed relationship between juvenile submission and territorial male aggression, it is possible that SC rate varies with the frequency of territorial male aggression. Additionally, territorial male aggression toward juveniles in spring may influence juvenile movement among groups. Juvenile males are seemingly expelled earlier than juvenile females (Franklin 1983), and as a result, may exhibit SCs more frequently or for longer duration than juvenile females. Relative size and/or age of juveniles may also influence when they are expelled.

Theoretical treatments of parent-offspring conflict in mammals have focused on the timing of resource termination (e.g. milk) (Trivers 1974, 1985, MacNair and Parker 1978, Parker 1985, Tokuda and Seno 1994). In guanacos, aside from rejected suckling attempts, there appears to be little overt conflict between mother and offspring. As offspring mature they nurse less frequently, and, in essence, wean themselves (Garay et al. 1995, Sarno and Franklin submitted). The conflict between territorial males and juveniles, however, is overt, intense, and potentially injurious to juveniles. In

fact, we observed 1 instance of a territorial male killing a yearling in an attempt to expel it from the family group. Juveniles seemingly attempt to retain access to the territorial male's resource (territory), by using SCs at a time when it may be advantageous for territorial males to terminate such access. Of all the advantages gained by offspring remaining in groups longer, increased parental care may be the most important. A possible consequence of prolonged parental care may be greater survival and or reproductive success. Since territorial males generally do not regulate the number of animals on their territories, adult females may leave under crowded conditions, and males could lose potential reproductive opportunities.

The overall goal of this study is to understand the evolutionary and ecological significance of juvenile appeasement of adult male aggression and how it relates to the duration of parental care. We propose 4 basic questions, 2 from the perspective of territorial males and 2 from the perspective of juveniles: 1) Do territorial males direct more aggression toward juveniles of one sex, larger and/or older juveniles, or more or less submissive juveniles? 2) Does territorial male aggression influence movement of juveniles among family groups in spring and appear to be a proximate factor influencing juvenile dispersal? 3) Do juvenile males and females differ in the development, frequency of

displaying, and type of submissive crouches?, and 4) Does the frequency of submissive crouches by juveniles influence the number of groups that they visit during spring and also influence expulsion from family groups? Additionally, is there a relationship between territorial male aggression and juvenile submission in spring?

### Methods

The study was conducted from 20 November 1990 to 15 January 1994 in Torres del Paine National Park (51°S, 72°55'W), an International Man and Biosphere reserve located in the eastern foothills of the Andean mountain range of southern Chile. The park encompasses 2,400 km<sup>2</sup> and provides almost undisturbed habitat for wildlife. The study area was a 46 km<sup>2</sup> "peninsula" ranging from 200-400 m in elevation bordered by large lakes to the south, north, and west, and a sheep ranch to the east. The landscape was open with rolling hills, vegetation was generally < 1 m high, and animals were easily observed. Grasses (Festuca gracillana, Anarthrophyllum patagonium) and shrubs (Mulinum spinosum, Senecio patagonicus, and Berberis buxifolia) dominated this pre-andean steppe (Pisano 1974). Habituation to humans of this protected population facilitated approach on foot to within 5 to 10 m of guanacos without their retreat.

We captured and marked newborn chulengos (Franklin and Johnson 1994) between 18 November and 10 December each year

from 1990 to 1992. We sexed, weighed, and tagged chulengos in both ears with individually numbered plastic ear tags. Additionally, we fitted most with radio-transmitters mounted on expandable collars (modified from Keister et al. 1988). We captured 99 chulengos in 1990, 100 in 1991, and 98 in 1992. We observed all randomly located focal juveniles for 1 hr from 0830-1800 during summer (December-February), fall (March-May), and spring (September-expulsion), and from 1000-1600 during winter (June-August). Juveniles were located based upon the previous day's visual sightings or radio-telemetry locations. We also collected data on other marked juveniles present in the group (see Altmann 1974 for a detailed explanation of focal subgroup sampling). One to four observers were in the field year-round.

Individuals surviving to age 1 lived most of their first year during the calendar year following their year of birth. For example, animals from the 1990 cohort that survived to age 1, lived during the summer, fall, winter, and spring of 1991. Because the birth season began on approximately 15 November of each year, we classified all chulengos as yearlings on 15 November of the year following their birth year.

During SCs, we categorized tail position of juveniles from 0-5: 0=tail down, 1=tail horizontal, 2=tail above horizontal, 3=tail vertical, 4=tail forward curl (greater than 90° but not touching the back), and 5=tail full forward curl

(tail curled and touching the back). The position of the neck ranged from 0-2: 0=neck vertical (normal standing posture), 1=neck extended in a horizontal plane (even with the height of the shoulders), and 2=neck fully extended below the shoulders in a long S-shape in which part of the neck may or may not have contacted the ground. Body position also ranged from 0-2: 0=legs unbent (animal standing upright), 1=legs bent  $\leq 45^\circ$  at the knees, and 2=legs bent  $> 45^\circ$  at the knees. We also categorized territorial male aggression as low (ear threats behavior in which a male lowered its ears), medium (spitting and chasing juvenile), and high (ramming juvenile with chest, biting, kicking, and attempting to suffocate juvenile by forcing it to the ground).

We documented the number of SCs/hr, distance between juveniles and territorial males during SCs, duration of SCs, tail, neck, and body position, the number of FSCs, the frequency and type of aggressive interactions of territorial males toward juveniles, group size, group location, whether or not a juvenile accompanied its mother, and juvenile expulsion date. We determined expulsion date by reviewing our location data and noting the last day that each juvenile was observed with its mother in a family group. Juvenile males generally entered adult male groups upon expulsion. Juvenile females either wandered around alone, formed yearling female groups, or attempted to enter another family group.



We calculated sample size for submissive crouch/aggression data (i.e. data analyzed by t-test and ANOVA) based upon the number of marked juveniles observed during a given time period, not upon the number of observations for each animal. Because the individual was the unit of measure, we believe that our approach best describes the means and variances of our variables.

We used Student's t-test to examine differences between juvenile males and females in: mean number of SCs/hr, mean duration of SCs, and mean distance of juveniles from territorial males during SCs, mean number of groups/month that juveniles moved among, and the mean number of aggressive interactions/hr by territorial males toward juveniles.

We used logistic regression to relate the occurrence or absence of SCs during an observation to explanatory variables. Possible covariates were juvenile sex, whether a juvenile accompanied its mother, group size, number of young of the year in the group, number of non-young of the year in the group (depending on the age of a particular cohort this could be chulengos or yearlings), season, birth weight, and number of times observed on an adult male's territory. We conducted multiple t-tests (i.e. month-season) without using Bonferroni control because we did not observe the same animals in each month-season.

We used standard ANOVA techniques to compare the mean

number of SCs/hr of juveniles that were expelled below (early) and above (late) the median expulsion date (6 December), or not expelled. We also examined the mean number of aggressive interactions/hr that early, late, and unexpelled juveniles received from territorial males. In order to observe potential differences between juvenile males and females in the intensity of SCs, we analyzed the proportion of various tail, neck, and body positions using chi-square analysis. In order to generate sufficient sample sizes for this analysis, we pooled observations within seasons. Additionally, we used chi-squared tests to analyze the number of FSCs by juvenile males and females, and to determine if the number of aggressive interactions that juveniles received from territorial males depended upon if they initiated a SC or FSC. We also analyzed the proportion of male and female juveniles that were expelled during two week intervals from 1 November until 31 December. We grouped observations into 2-week intervals with the intent of maintaining large enough sample sizes for analysis, yet restricting the interval sufficiently to observe potential differences in the timing of expulsion of juvenile males and females. The first day on which we located an expelled juvenile was 1 November, and  $\approx 90\%$  of expelled juveniles were expelled by 31 December.

We used Pearson correlation to evaluate the relationships between: the mean number of SCs/hr and the number of groups

that juveniles were observed in during spring, the number of groups juveniles were observed in during spring and expulsion date, the mean number of aggressive interactions/hr by territorial males and mean number of SCs/hr by juveniles, the mean number of aggressive interactions/hr by territorial males and juvenile expulsion date, and the mean number of SCs/hr of juveniles and expulsion date. All statistical analyses were conducted using SAS software (SAS Institute, Inc., 1989). The probability values of some of our results fell between 0.051-0.067, although not statistically significant at  $\alpha = 0.05$ , we believe that they are biologically meaningful.

## **Results**

### **Submissive crouches and juvenile movement among groups**

Juvenile males displayed more SCs/hr than females in every month-season, however, these differences were significant only in fall ( $t = 2.56$ ,  $df = 162$ ,  $P = 0.011$ ), September ( $t = 2.32$ ,  $df = 131$ ,  $P = 0.022$ ), and November ( $t = 2.08$ ,  $df = 86$ ,  $P = 0.040$ ; Figure 1). In October, the data suggest that juvenile males tended to display substantially more SCs/hr than juvenile females ( $t = 1.85$ ,  $df = 89$ ,  $P = 0.067$ ). The mean duration of juvenile male SCs was significantly longer than those of females in fall ( $t = 2.33$ ,  $df = 121$ ,  $P = 0.021$ ), September (unequal variance  $t = 2.52$ ,  $df = 67.1$ ,  $P = 0.043$ ), and November (unequal variance  $t = 2.72$ ,  $df = 58.4$ ,  $P = 0.009$ ) (Figure 2). Juvenile males were

Figure 1. Monthly-seasonal mean number of submissive crouches/hr by juvenile guanacos in Torres del Paine National Park, Chile from January 1991 to December 1993. Asterisk indicates significant difference (see text for test statistic and P value). Extending lines indicate standard error. Number above standard error bar represents sample size.

## Submissive Crouch Frequency

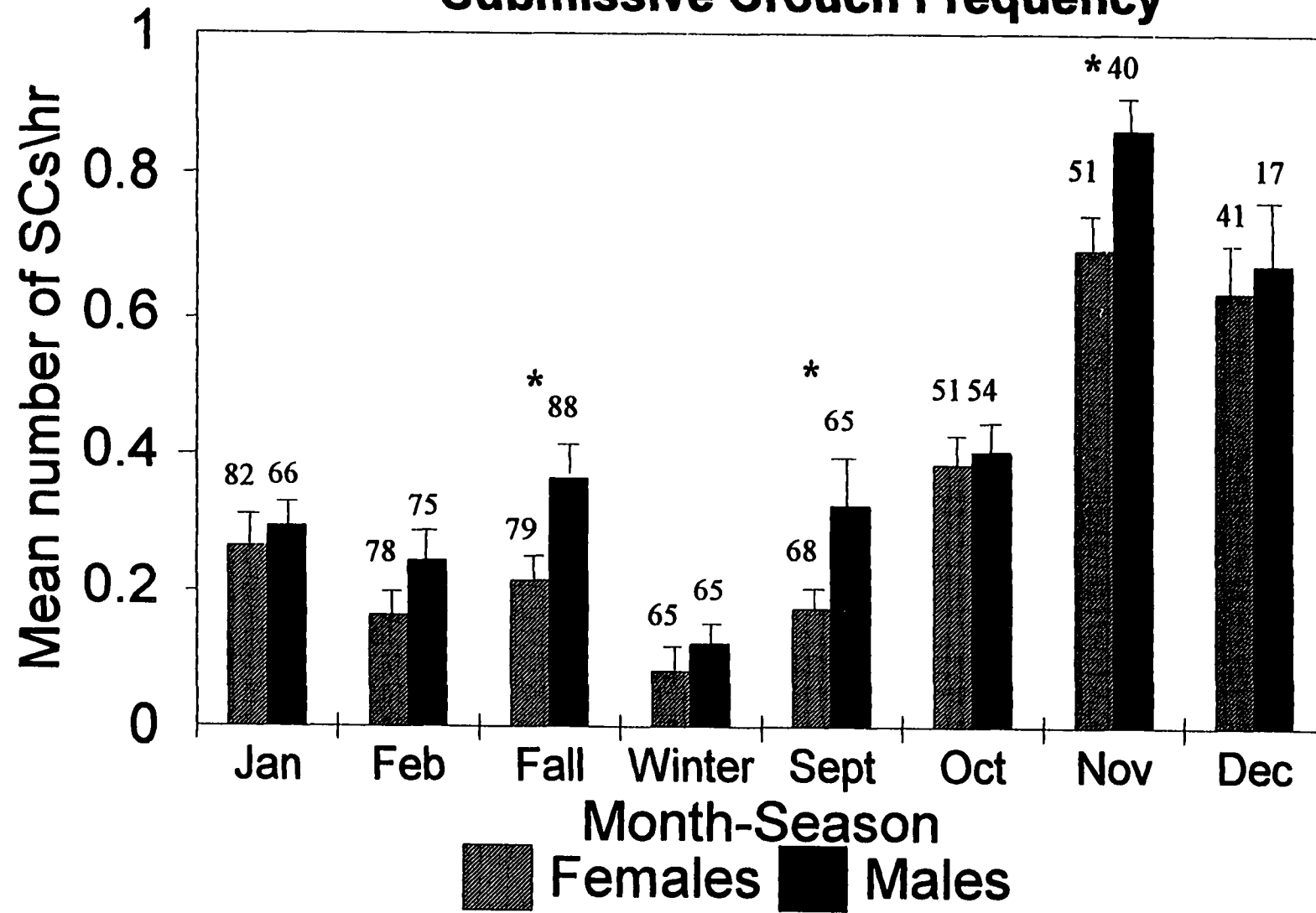
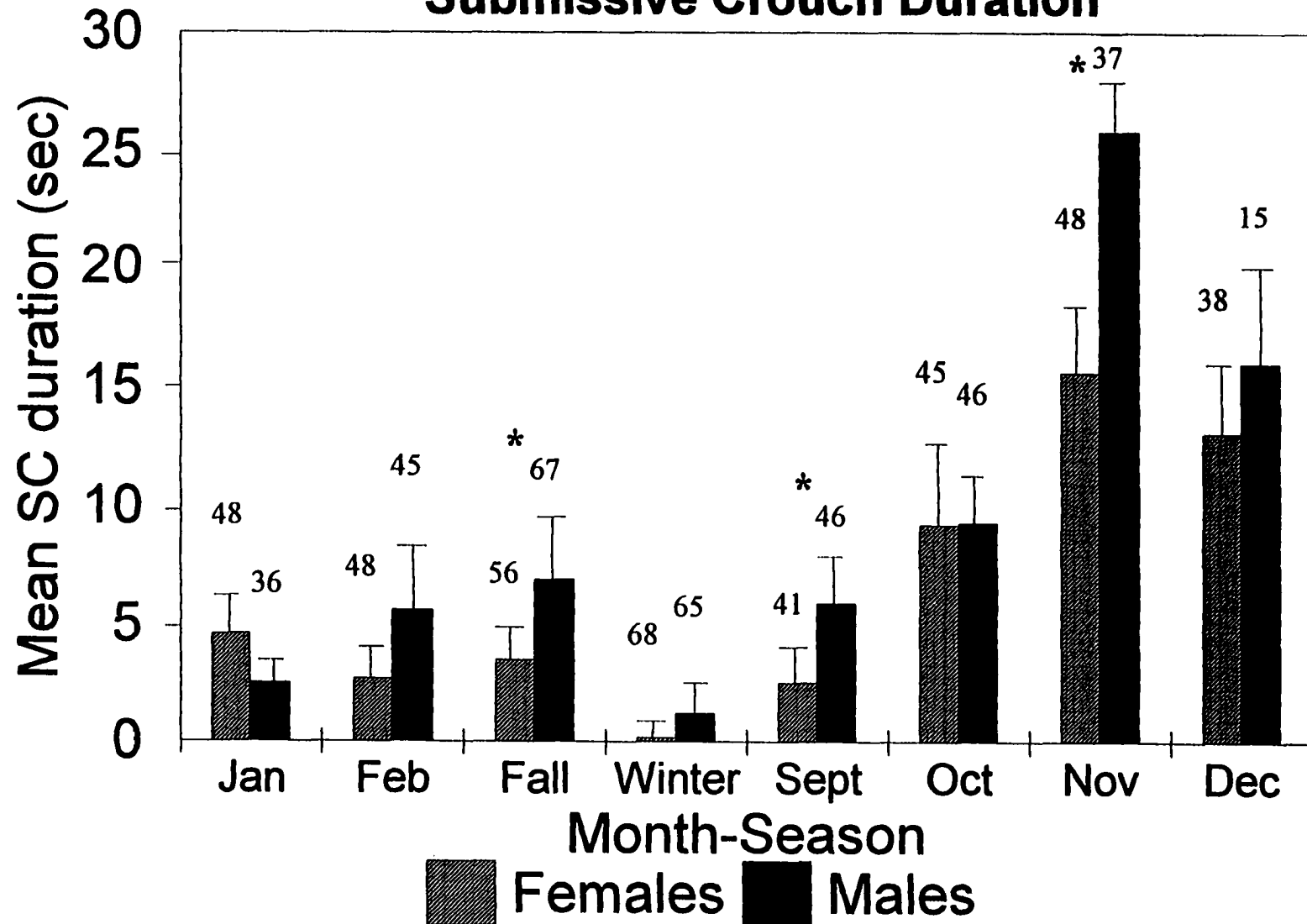


Figure 2. Monthly-seasonal mean duration of submissive crouches/hr by juvenile guanacos in Torres del Paine National Park, Chile from January 1991 to December 1993. Asterisk indicates significant difference (see text for test statistic and P value). Extending lines indicate standard error. Number above standard error bar represents sample size.

## Submissive Crouch Duration



farthest away from adult males during SCs in January and November (Table 1). The proportion of tail, neck, and body positions that juvenile males and females exhibited during SCs did not differ in every season (Table 2). When they did, however, juvenile females exhibited significantly less extreme tail, neck, and body postures in greater than expected frequencies, while juvenile males exhibited significantly more extreme tail, neck, and body postures in greater than expected frequencies.

The mean number of SCs/hr of yearlings that were expelled early ( $\bar{x} = 1.20$ ,  $SE = 0.44$ ,  $n = 21$ ), late ( $\bar{x} = 1.42$ ,  $SE = 0.36$ ,  $n = 52$ ) or not expelled ( $\bar{x} = 2.63$ ,  $SE = 0.71$ ,  $n = 20$ ) were almost significantly different and increased with time spent in family groups before expulsion ( $F = 2.84$ ,  $df = 2, 93$ ,  $P = 0.062$ , Figure 3). There was, however, no sex by median expulsion date interaction ( $F = 1.07$ ,  $2, 93$ ,  $P = 0.366$ ). Juvenile males ( $n = 36$ ) and females ( $n = 27$ ) did not differ in the number of FSCs to territorial males ( $\chi^2 = 0.57$ ,  $df = 1$ ,  $P = 0.550$ ).

Animal sex, group size, and season were related to the odds of a juvenile displaying a SC (Table 3). Juvenile males visited more family groups than juvenile females in every month-season except December. In fall (unequal variance  $t = 4.47$ ,  $df = 124.9$ ,  $P = 0.001$ ) and November ( $t = 3.131$ ,  $df = 70$ ,  $P = 0.001$ ) these differences were significant (Figure



Table 1. Mean distance between juvenile guanacos and territorial males during submissive crouches in Torres del Paine National Park, Chile, January 1991 to February 1994. Asterisk indicates significant difference between males and females.

Month	Sex	Distance (m)	SE	N
January*	Females	5.0	0.86	33
	Males	10.0	2.31	31
February	Females	4.0	1.21	27
	Males	6.0	0.84	33
Fall	Females	5.0	0.77	46
	Males	7.0	1.19	64
Winter	Females	3.0	1.82	24
	Males	1.0	0.35	33
September	Females	4.0	1.06	25
	Males	7.0	1.61	42
October	Females	14.0	3.01	39
	Males	13.0	2.43	44
November**	Females	19.0	2.27	46
	Males	28.0	3.75	37

\* (unequal variance  $t = 2.25$ ,  $df = 38.2$ ,  $P = 0.030$ )

\*\* (unequal variance  $t = 2.010$ ,  $df = 60.8$ ,  $P = 0.049$ )

Table 2. Comparisons of the proportion of tail, neck, and body positions between juvenile male and female guanacos during submissive crouches in Torres del Paine National Park, Chile from January 1991 to January 1994.

Season	$\chi^2$ Tail	df	P	$\chi^2$ Neck	df	P	$\chi^2$ Body	df	P
Summer	11.1	5	0.05	2.2	2	0.34	0.04	2	0.98
Fall	31.2	5	0.00	17.7	2	0.00	7.04	2	0.03
Winter	3.78	5	0.12	2.75	2	0.10	0.00	2	1.00
Spring	8.78	5	0.12	6.33	2	0.04	21.9	2	0.00

Figure 3. Mean number of submissive crouches/hr of juvenile guanacos in Torres del Paine National Park, Chile not expelled, or expelled below (early) and above (late) the median expulsion date. Interval ranges from 1 November to 31 December each year from 1991 to 1993.

## Juvenile Expulsion

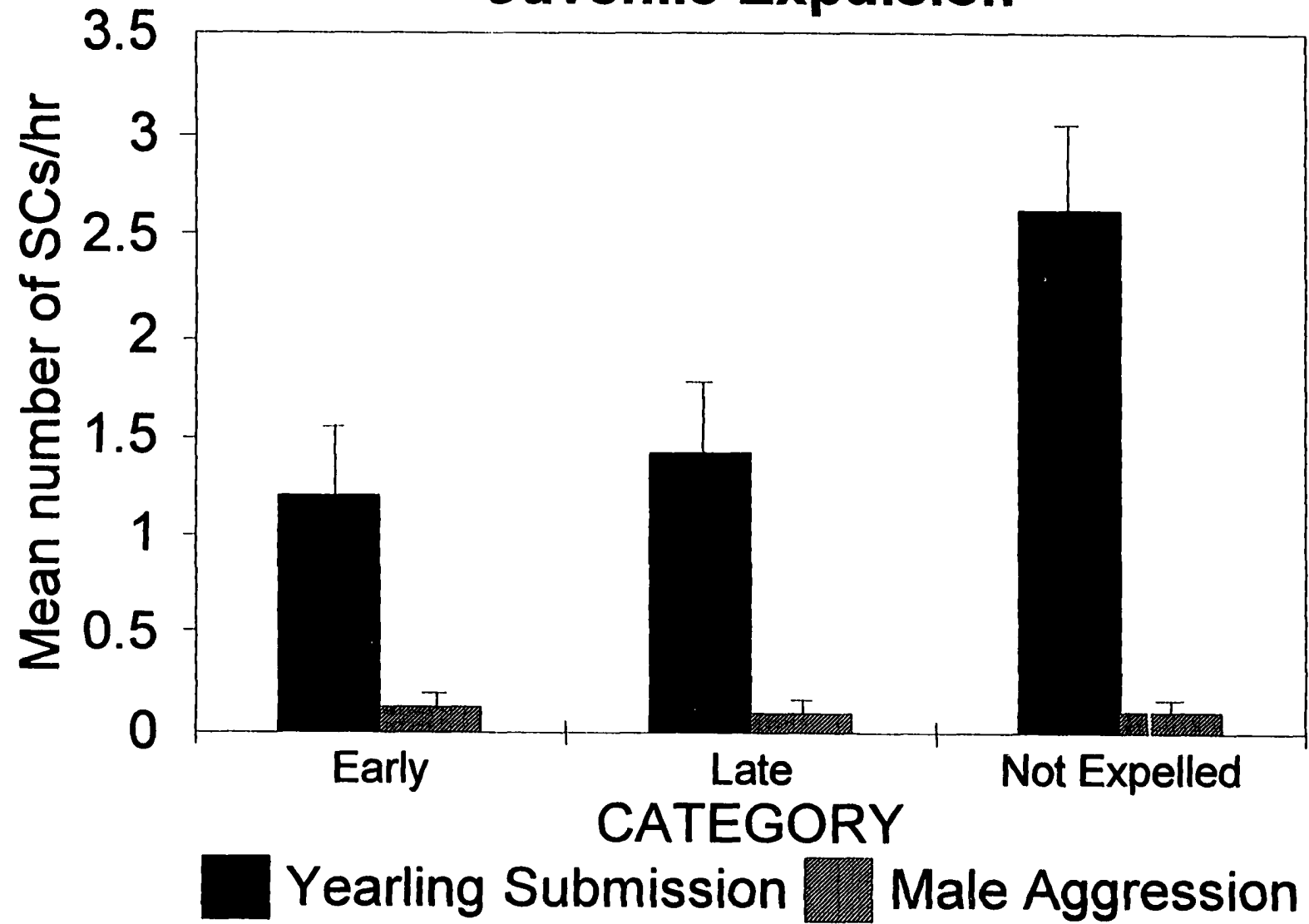


Table 3. Parameters of a logistic regression model relating covariates to the likelihood that a juvenile guanaco would exhibit a submissive crouch in Torres del Paine National Park, Chile, January 1991 to February 1994. Asterisk denotes that males were coded as 0 and females as 1.

Parameter	$\beta$	SE	Wald $\chi^2$	P	Odds Ratio
Juvenile sex*	-0.353	0.123	8.24	0.004	1.423
Accompany mother	0.594	0.345	2.96	0.085	1.812
Group size	-0.019	0.004	17.7	0.0001	0.981
Number of chulengos	-0.017	0.022	0.61	0.435	0.983
Number of yearlings	-0.024	0.032	0.55	0.458	0.977
Fall	0.025	0.179	0.02	0.890	1.026
Winter	-0.024	0.379	0.004	0.950	0.976
Spring	0.520	0.160	10.6	0.001	1.681
Birth weight	-0.093	0.089	1.07	0.300	0.912
Association\w territorial male	0.037	0.095	0.156	0.693	1.038

4).

#### Aggression by territorial males

Territorial males initiated more aggressive interactions/hr toward juvenile males than females throughout most of the year, but these differences were significantly different only in November (unequal variance  $t = 2.36$ ,  $df = 88.7$ ,  $P = 0.021$ ) (Table 4). There was no significant difference in the mean number of aggressive interactions/hr by territorial males toward juveniles that were expelled early ( $\bar{x} = 0.13$ ,  $SE = 0.056$ ,  $n = 21$ ), late ( $\bar{x} = 0.11$ ,  $SE = 0.034$ ,  $n = 52$ ), or not expelled ( $\bar{x} = 0.11$ ,  $SE = 0.051$ ,  $n = 20$ ;  $F = 0.11$ ,  $df = 2, 93$   $P = 0.893$ , Figure 3), nor was there a sex by expulsion date interaction ( $F = 1.05$ ,  $df = 3, 93$ ,  $P = 0.376$ ). Additionally, territorial males directed significantly more aggressive interactions (34%) toward juveniles that initiated FSCs, than toward juveniles that exhibited SCs (2.4%;  $\chi^2 = 97.1$ ,  $df = 1$ ,  $P < 0.0001$ ). Territorial males also exhibited the greatest proportion of low, medium, and high aggression toward juveniles in spring (Figure 5).

#### Aggression, submission, movement among groups, and expulsion

When territorial males actually exhibited aggression toward juveniles, mean aggression rate was a good predictor of juvenile female submission rate ( $R^2 = 0.50$ ,  $P = 0.002$ ,  $N = 16$ ), but not for juvenile male submission rate ( $R^2 = 0.02$ ,  $P = 0.02$ ,  $P = 0.884$ ,  $N = 20$ ; Figure 6). There was no significant

Figure 4. Monthly/seasonal mean number of groups that juvenile guanacos moved among in Torres del Paine National Park, Chile from January 1991 to December 1993. Asterisk indicates significant difference (see text for test statistic and P value). Extending lines indicate standard error. Number above standard error represents sample size.

## Juvenile Movement Among Groups

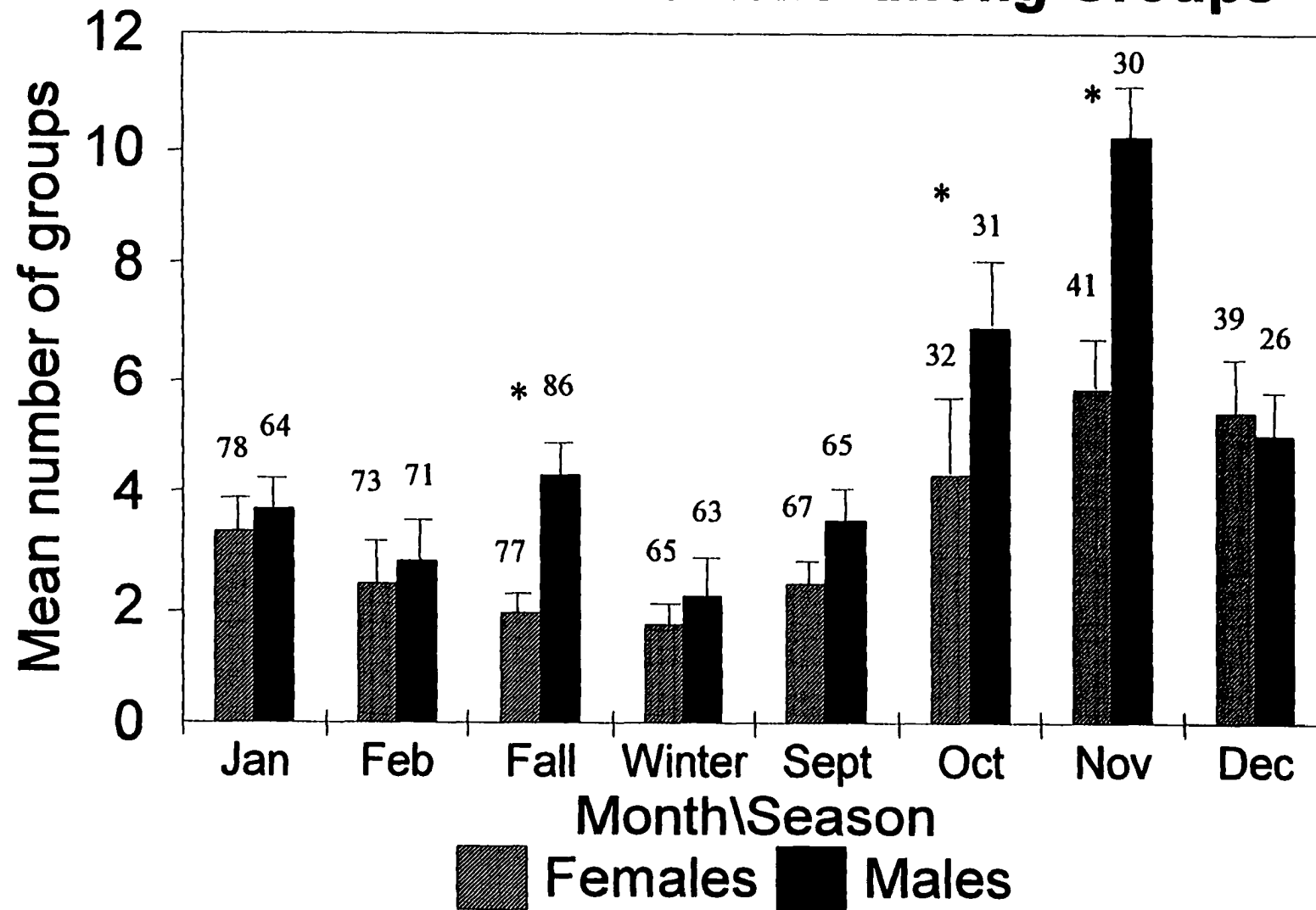




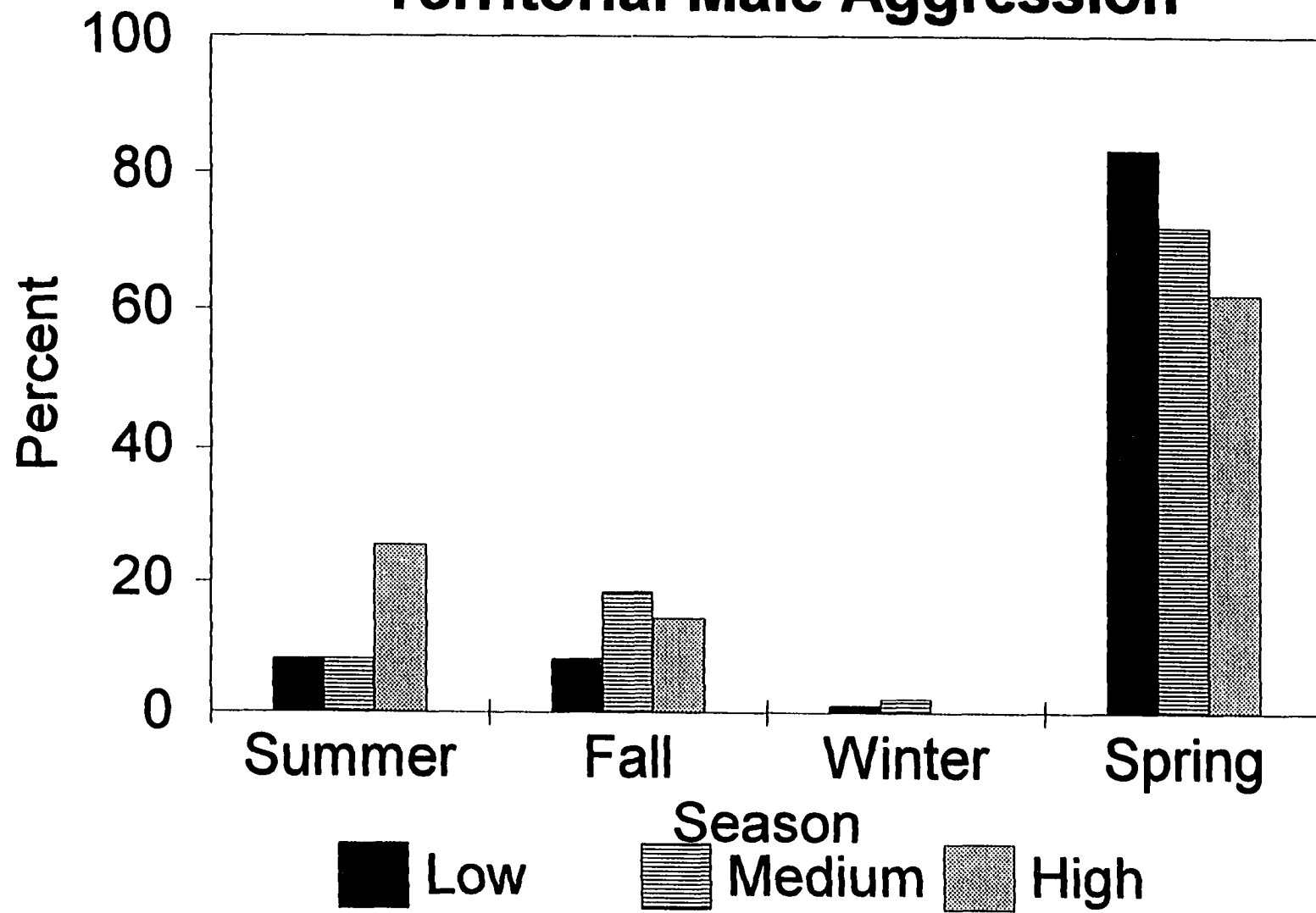
Table 4. Mean monthly frequency of aggression by territorial males toward juvenile guanacos from birth to expulsion in Torres del Paine National Park, Chile from January 1991 to February 1994. Asterisk after month indicates significant difference between males and females. See text for test statistic and P value.

Month	Sex	Mean	SE	N
January	Females	0.08	0.024	80
	Males	0.04	0.015	78
February	Females	0.07	0.024	88
	Males	0.06	0.024	85
Fall	Females	0.04	0.013	158
	Males	0.07	0.014	167
Winter	Females	0.02	0.010	112
	Males	0.03	0.017	90
September	Females	0.08	0.028	77
	Males	0.09	0.027	82
October	Females	0.01	0.007	69
	Males	0.03	0.010	76
November*	Females	0.05	0.018	74
	Males	0.13	0.037	59
December	Females	0.06	0.026	56
	Males	0.03	0.015	44

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	Males	0.13	0.037	59
December	Females	0.06	0.026	56
	Males	0.03	0.015	44

# Territorial Male Aggression



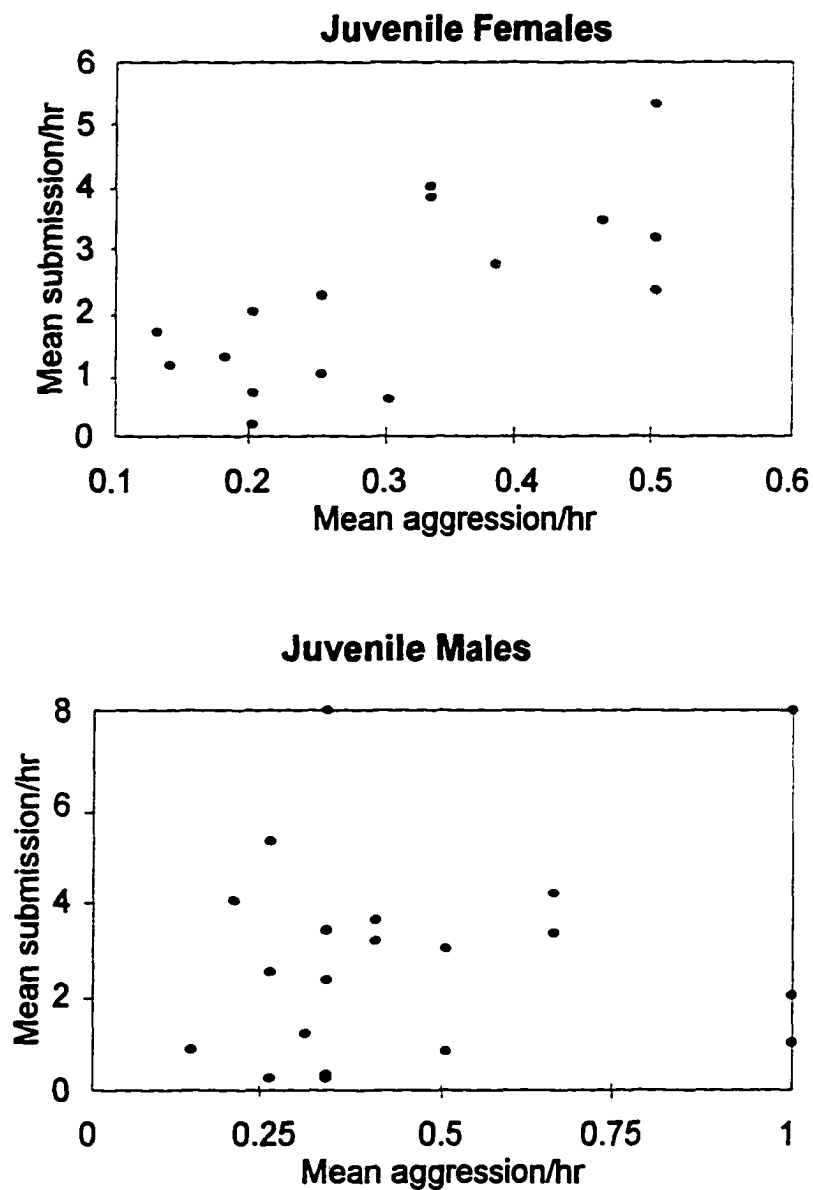


Figure 6. Plot of mean number of submissive crouches/hr of juvenile guanacos versus mean number of aggressive interactions/hr of territorial males in Torres del Paine National Park, Chile during spring of 1991 to 1993.

correlation in spring between the mean number of SCs/hr and number of groups that juvenile males and females visited ( $R_{\text{females}} = -0.002$ ,  $P = 0.987$ ,  $n = 89$ ;  $R_{\text{males}} = 0.041$ ,  $P = 0.699$ ,  $n = 90$ ). There was also no significant correlation between the mean number of aggressive interactions/hr by territorial males toward juveniles and the number of groups that juvenile females or males visited during spring ( $R_{\text{females}} = 0.081$ ,  $P = 0.445$ ,  $n = 91$ ;  $R_{\text{males}} = -0.027$ ,  $P = 0.794$ ,  $n = 90$ ).

The more groups that juvenile females visited the earlier they were expelled ( $R_{\text{females}} = -0.439$ ,  $P = 0.003$ ,  $n = 44$ ); this relationship was not observed for juvenile males, however ( $R_{\text{males}} = 0.009$ ,  $P = 0.985$ ,  $n = 49$ , Figure 7). The mean number of aggressive interactions/hr by territorial males was not strongly correlated with juvenile expulsion date ( $R_{\text{females}} = -0.148$ ,  $P = 0.339$ ,  $n = 44$ ;  $R_{\text{males}} = 0.149$ ,  $P = 0.307$ ,  $n = 49$ ), nor was the mean number of SCs/hr strongly correlated with expulsion date ( $R_{\text{females}} = 0.069$ ,  $P = 0.05$ ,  $n = 44$ ;  $R_{\text{males}} = -0.123$ ,  $P = 0.400$ ,  $n = 49$ ). Although a greater proportion of juvenile males were expelled earlier than juvenile females, there was no significant difference in the number of males and females that were expelled by 31 December ( $\chi^2 = 1.72$ ,  $df = 3$ ,  $P = 0.633$ ; Figure 8).

There was no difference in the birth weight (kg) of expelled ( $\bar{x} = 12.3\text{kg}$ ,  $SE = 0.206$ ,  $n = 73$ ) and unexpelled juveniles ( $\bar{x} = 12.2\text{kg}$ ,  $SE = 0.324$ ,  $n = 26$ ;  $t = 0.232$ ,  $df = 97$ ,

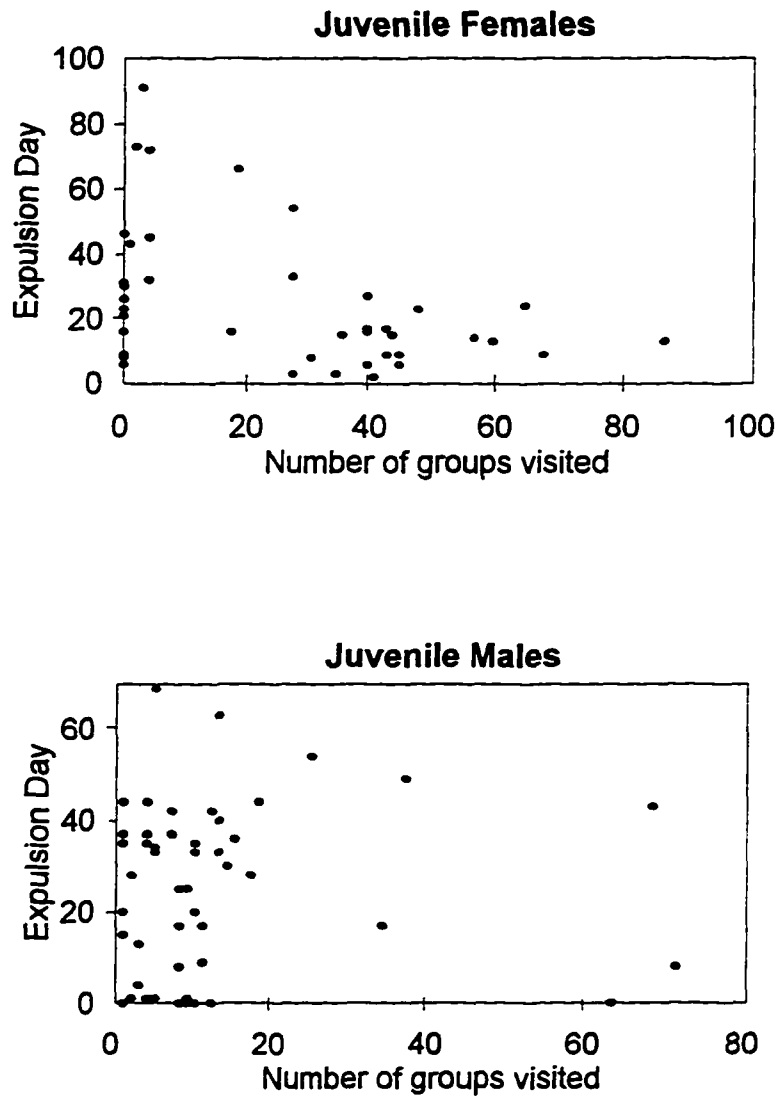


Figure 7. Plot of expulsion day of juvenile guanacos versus the number of groups visited during spring of 1991 to 1993 in Torres del Paine National Park, Chile.

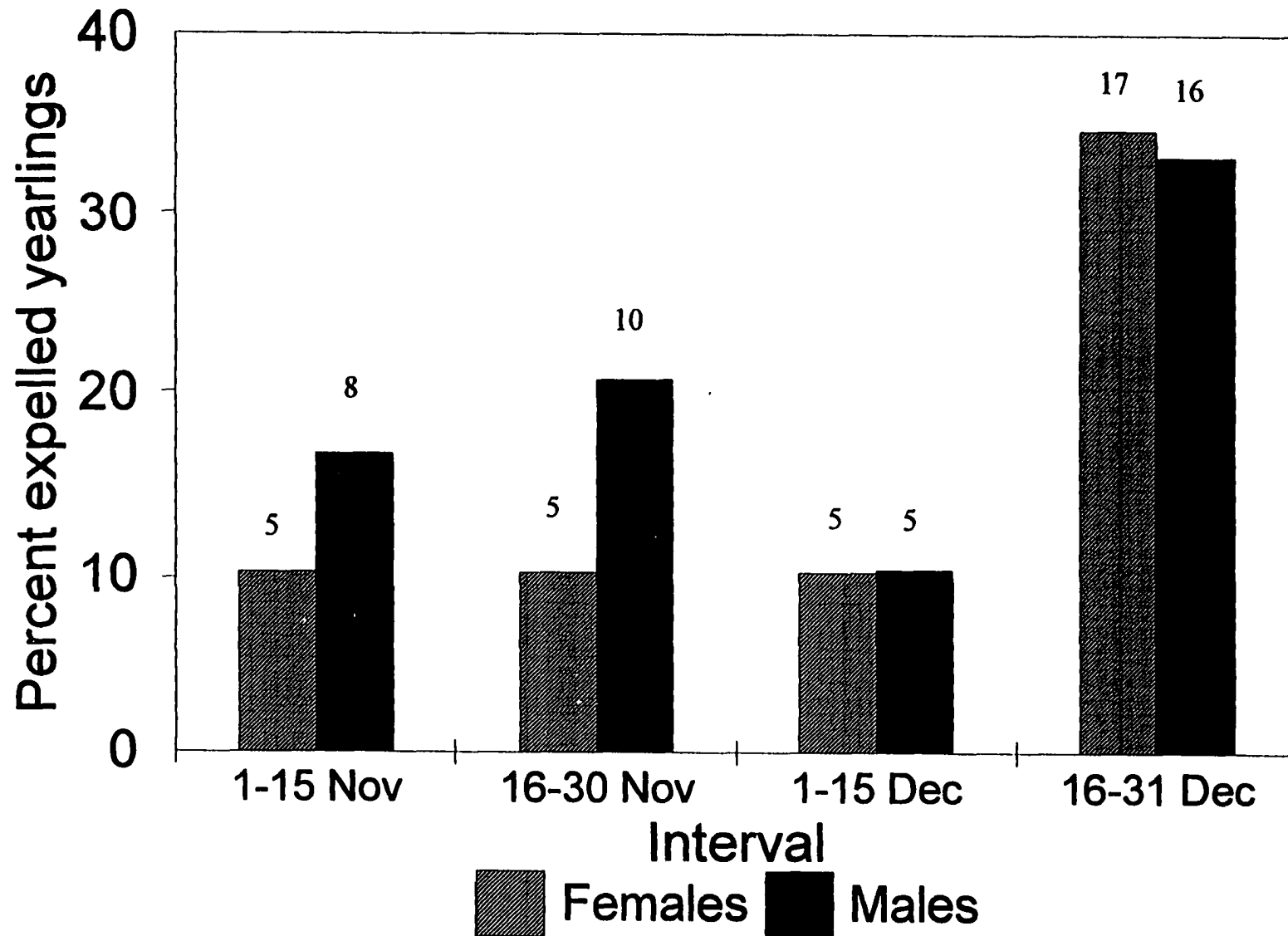
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There was no difference in the birth weight (kg) of expelled ( $\bar{x} = 12.3\text{kg}$ ,  $SE = 0.206$ ,  $n = 73$ ) and unexpelled juveniles ( $\bar{x} = 12.2\text{kg}$ ,  $SE = 0.324$ ,  $n = 26$ ;  $t = 0.232$ ,  $df = 97$ ,  $P = 0.82$ ). Additionally, the median birth date pooled across years of expelled (25 Nov) and unexpelled (26 Nov) juveniles differed by only 1 day. We are sure that at least 5 (19%,  $n = 26$ ) of the mothers of unexpelled juveniles were accompanied by a newborn compared to 3 (4%,  $n = 71$ ) of the mothers of expelled juveniles.

## Discussion

Fall, September, and November are important periods for guanacos in Torres del Paine (Franklin 1983, Ortega and Franklin 1995). In fall, family groups disband and

## Juvenile Expulsion





$P = 0.82$ ). Additionally, the median birth date pooled across years of expelled (25 Nov) and unexpelled (26 Nov) juveniles differed by only 1 day. We are sure that at least 5 (19%,  $n = 26$ ) of the mothers of unexpelled juveniles were accompanied by a newborn compared to 3 (4%,  $n = 71$ ) of the mothers of expelled juveniles.

### **Discussion**

Fall, September, and November are important periods for guanacos in Torres del Paine (Franklin 1983, Ortega and Franklin 1995). In fall, family groups disband and animals form large mixed groups until winter's end. The increased frequency and duration of SCs by chulengo males ( $\approx 4$  months old) in fall, prior to the dissolution of family groups might increase the likelihood that territorial males recognize particular individuals the following spring. The increase in SC duration by juvenile males in September (early spring) occurs as family groups form. It is again possible that chulengo males are more actively signaling their subordinate status to territorial males. The increase in both SC frequency and duration in November probably occurs because territorial males have started expelling juveniles.

The significantly greater distance between chulengo males and territorial males during SCs in January probably has little to do with deteriorating chulengo-territorial male social relations, but indicates the propensity of chulengo

males to wander farther from family groups (Prexl unpublished data). In November, however, the significant difference likely results from juvenile expulsion and increased aggression from territorial males. The trend toward more extreme tail (raised higher), neck (lower to ground), and body (crouching lower or lying on the ground) positions of juvenile males suggests that their interactions with territorial males were more intense than interactions between juvenile females and territorial males.

We previously mentioned why we conducted t-tests without Bonferroni adjustments for simultaneous comparison. Additionally, the data for mean number of SCs/hr and mean duration of SCs show that juvenile males were higher in every month-season except one. Also, differences between juvenile males and females in the mean distance between juveniles and territorial males occurred when juvenile males were, on average, twice and one-third farther from territorial males than juvenile females.

Animal sex, group size, and season influenced whether juveniles exhibited a SC. The odds ratio of the logistic regression for sex indicates that juvenile males were more likely to exhibit SCs. This is supported by the data, because in all months-seasons juvenile males exhibited more SCs/hr than juvenile females. As group size increased, the likelihood of an individual exhibiting a SC decreased.

Juveniles in larger groups were probably able to "hide" from territorial males and had fewer encounters with them.

Juveniles were also more likely to exhibit SCs during spring. The increase in odds is also supported by the increase in SC frequency from September to November, and is likely associated with escalating territorial male aggression toward juveniles.

The greater movement among groups of male chulengos in fall is also intriguing. Chulengo movement among groups is governed by the movement of adult females. Is greater movement by adult females with sons a strategy to familiarize male offspring with as many territorial males as possible, or does increased movement result from brief periods on a males' territory before aggression increases to the point where adult females leave? More frequent and longer SCs, and greater movement among groups, might further serve to reduce aggression from territorial males. Greater movement among groups by adult females-juvenile males in November is most likely related to escalating territorial male aggression and juvenile expulsion.

An alternative explanation is that greater movement among groups is driven by nutritional requirements. We doubt that adult females with sons moved more frequently in search of food to satisfy differential energetic requirements, however, because both sexes have nearly equal birth weights and appear to receive equal amounts of energy from mothers (Franklin and

Johnson 1994, Sarno and Franklin Submitted). Juveniles that never exhibited SCs generally moved among 2 to 3 times as many groups as did juveniles that exhibited SCs. Perhaps territorial males were less tolerant of seemingly less submissive individuals.

### **Territorial Male Aggression**

Although the frequency of aggression toward 2-3 month old chulengos was relatively high in summer (Jan and Feb), we do not believe that it was indicative of systematic aggression from territorial males toward chulengos. Territorial males rarely initiated any type of interaction with young chulengos. Most of the aggression resulted from chulengos attempting to follow and play with territorial males. Males generally used ear threats (low aggression) and retreated from chulengos during such encounters. Even at this young age it is conceivable that playing with territorial males has a functional aspect. Since some chulengos were already initiating SCs, playing with territorial males may have fostered familiarization between territorial males and chulengos.

The relatively high levels of territorial male aggression toward chulengos in fall was surprising. We can offer no logical explanation why this occurred. During winter, aggression decreased probably because animals are obligated to form large mixed groups due to environmental conditions. The

overwhelming proportion of low, medium, and high aggression in spring is congruent with the decreasing tolerance of juveniles by territorial males. Although significantly different only in November, territorial male aggression toward juvenile males was consistently higher than that toward juvenile females from fall to November. This may explain why juvenile males exhibited a higher frequency and longer duration of SCs from February (3 months old) to December (13 months old), and also moved among more groups during fall and November.

Perhaps the efficacy of FSCs can be questioned, because juveniles that initiated them received significantly more aggressive interactions from territorial males than juveniles that displayed SCs. This apparent cost may explain why juveniles do not initiate FSCs more frequently. Conversely, the potential benefit of initiating FSCs may increase the time in family groups before expulsion. Although sample size is small ( $n = 15$  animals), 66% of juveniles that initiated FSCs were expelled late or not expelled at all. Submissive behavior has been demonstrated to reduce aggression from conspecifics (Lorenz 1966, Koutnik 1980, York and Rowell 1988), and/or promotes familiarity among unrelated individuals (Bernstein 1964, 1969, Goodall 1986, Nishida and Hiraiwa-Hasegawa 1985, Reynierse 1971, Poole 1973). Remaining in family groups longer would tend to increase the number of juveniles that exhibit FSCs. Why we did not observe more

juveniles exhibiting FSCs is puzzling.

**Aggression, submission, juvenile movement, and expulsion**

The lack of differential aggression by territorial males toward juveniles that were expelled early, late, or not expelled, coupled with the weak correlation between the frequency of territorial male aggression and juvenile expulsion date, suggests that the mean rate of territorial male aggression is not a good predictor of juvenile expulsion. Expulsion events appear to be of short duration and are marked by intense aggression (biting, kicking, and attempted suffocation of juveniles) by territorial males. In support of this we only witnessed 7 marked animals expelled during the entire study. When territorial males decide to expel given juveniles is not clear and is probably more complex than previously thought.

Adult females likely play an important but mostly passive role in influencing the expulsion date of their offspring. During the expulsion season juveniles often followed their mothers closely. Additionally, after encounters in which territorial males demonstrated aggression, juveniles at times ran to their mothers and nursed ( $n = 53$ ) in an apparent effort to seek protection and demonstrate their young age to males. Adult females at times also defended ( $n = 19$ ) their offspring from territorial males during expulsion attempts.

Juvenile females that moved less in spring (i.e. resided

longer in fewer groups) were expelled later. Remaining longer in family groups may have increased familiarity with territorial males, reduced aggression, and ultimately increased the period of parental care. It is also possible that these individuals were sired by one of the territorial males whose territory they resided on. Why this relationship was not more strongly correlated for juvenile males is intriguing and suggest that other factors (e.g. generally more aggression toward juvenile males) are operating.

Why are juvenile males generally expelled before juvenile females? There is no apparent relationship between movement among groups, SC frequency, or mean number of aggressive interactions/hr by territorial males with expulsion date of juvenile males. Additionally, at expulsion, juvenile males are approximately half as large as territorial males, and are physically unable to reproduce. Our best guess results from considering the ecology of territorial males during spring. The mean rate of aggressive interactions/hr by territorial males toward all other adult males begins increasing in September and peaks in early to mid-December (Jurgensen 1985, Wilson and Franklin 1985, Franklin unpublished data). This aggression centers around territorial defense and mating opportunities. We suggest that rising hormone levels in territorial males increase their aggression (and decrease tolerance) toward all other males, resulting in the earlier

expulsion of juvenile males.

Perhaps an equally important consideration is why juvenile females are generally expelled later than males. The reproductive interests of territorial males may be operating. By permitting juvenile females to remain longer in family groups, territorial males might be "encouraging" juvenile females to return to the adult males' territory the following year when they are able to reproduce. In support of this idea, approximately 35% of yearling females were not expelled compared to 19% of yearling males by the end of the expulsion season (31 Dec).

Although there was no strong correlation between SC frequency and expulsion date per se, there were noticeable differences in SC frequency among juveniles that were expelled early, late, or not expelled. The SC frequency of unexpelled juveniles was more than double that of juveniles expelled early, and was almost double that of juveniles expelled late. Albeit these differences are not statistically different ( $P = 0.062$ ), we believe that they are biologically meaningful.

There is an apparent adaptive feature to exhibiting a relatively higher frequency of SCs, because individuals who did so remained in family groups longer before expulsion or were not expelled. Although employing SCs to reduce territorial male aggression appears to be a strategy for all juveniles, some individuals undoubtedly exhibit them more



frequently than others. This explanation implies some behavioral plasticity. We can also extend this idea to our interpretation of the odds ratio from the logistic regression. Perhaps the increased odds of juvenile males exhibiting a SC results from some innate behavioral difference between the sexes.

Since most yearlings are expelled between 16-31 December, why do SC frequency and duration, yearling movement among groups, and territorial male aggression toward yearlings decrease in December? Territorial male aggression likely decreases in response to a switch to mating and territorial defense activities. As a result, territorial males interact less often with yearlings and direct less aggression towards them. Hence, SC frequency and duration, and yearling movement among groups decreases. It is not until after the peak of the mating season (15 Dec) that territorial males expel the greatest proportion of yearlings. It would be adaptive for territorial males to no longer tolerate the presence of yearlings after they have mated with their mothers. The reproductive interests of territorial males may not be the only factor operating, however. Chulengos do not begin feeding regularly until approximately 2 to 4 weeks after birth. There is a period that the rumen needs to develop and begin functioning. Is it coincidental that most of the yearlings are expelled during the period when the majority of

chulengos begin feeding regularly? Competition for food resources is likely most intense at this juncture. Yearling expulsion may ultimately be driven by limiting food resources, which would support Dobson's (1982) competition for environmental resources hypothesis.

Assuming equal growth rates, we hypothesized that larger juveniles (i.e. heavier at birth) would be expelled before smaller juveniles. This did not occur. Another indication of size or maturity we considered was birth date. There appears to be no trend, however, among unexpelled yearlings for being born later. Although sample sizes are small, the data suggest that yearlings have a greater likelihood of being expelled if their mothers have produced a newborn chulengo. This trend was also observed on Tierra del Fuego (Franklin, unpublished data).

### **Conclusions**

In conclusion, it tentatively appears that juvenile guanacos increase their time in family groups, hence extending the period of parental care, by means of subordinate behavior. The data suggest that the most frequently submissive individuals remained in family groups longest before expulsion. Increased parental care could ultimately increase survival and reproductive success. Besides utilizing SCs, juvenile females may be able to delay expulsion by remaining in given family groups longer. Genetic relatedness and if the

juvenile's mother has produced a newborn may also influence if and when a juvenile is expelled. Although juvenile males are generally more submissive than juvenile females, it apparently does not have a widespread effect on increasing a juvenile male's time in the family group before expulsion. As a result, more juvenile males than females are generally expelled. Perhaps territorial males allowed juvenile females to remain longer on territories, thus "encouraging" their return the following year.

The late expulsion (16-31 Dec) of the majority of yearlings (13 months old) is most intriguing. Territorial males could expel juveniles earlier in the season, but adult females would probably accompany their offspring, and territorial males might lose many mating opportunities. It could be in the reproductive interests of territorial males to permit the majority of juvenile females to remain on their territories for a certain period of time. Competition for food is likely most intense at this juncture, however, and juvenile expulsion may ultimately be driven by limiting food resources, which would support Dobson's (1982) competition for environmental resources hypothesis. This certainly appears to be the case for the other wild South American camelid, the vicuña (Vicugna vicugna), because juvenile males are expelled at 6 months of age at the onset of the dry season when primary productivity is beginning to decrease (Franklin 1979).

**Future research**

More definitive answers regarding yearling expulsion will only come with an experimental approach, one in which we can control adult female movement, be assured of juvenile paternity, and manipulate food supply. Enclosures would allow investigators to control movement of adult females and offspring, while providing insight into whether time with a given territorial male decreases aggression and delays expulsion. Additionally, the influence of genetic relatedness in mediating territorial male aggression and juvenile expulsion could be more effectively examined. We initially attempted to determine genetic relatedness among territorial males and chulengos (Sarno et al. 1996). Because of the large number of territorial males and frequent movement among groups of adult females and offspring, the number of potential consanguineous relationships were too few to warrant further analysis. One could ascertain if the production of a newborn influences the likelihood of yearling expulsion. We suspect that the rate of territorial male aggression toward a particular juvenile rises considerably shortly before (1 or 2 days e.g.) expulsion. Finally, the amount of food would need to be manipulated in order to observe the effect on the timing of expulsion. Having animals in a captive setting and carefully controlling the number of animals in each enclosure would allow investigators to examine the influence that family

group size has on juvenile expulsions.

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## CHAPTER 4. GENERAL CONCLUSIONS

### General Discussion

Patterns of maternal expenditure in juvenile guanacos do not support the models of Trivers and Willard (1973) and Maynard-Smith (1980), because adult females appear to expend equal amounts of energy on sons and daughters; there were no significant differences in either birth weight or suckling behavior of juvenile males and females. There was a significant negative correlation between chulengo birth weight (a measure of pre-birth maternal expenditure) and population size. As birth weight decreased, population size increased. The effects of population density on growth, fecundity, birth weight, suckling time, and survival have been demonstrated in other species of mammals (Klein 1968, Caughley 1970, Geist 1971, Grubb 1974, Sinclair 1977, Clutton-Brock et al. 1982, Skogland 1984). There also appears to be a negative relationship between population size and suckling time, but more data are needed. In some situations, a proximate cause like population size could overshadow the importance of the ultimate causes theorized to result in differential maternal expenditure on sons and daughters.

Our results support Byers and Moodies' (1990) hypothesis that the level of reproductive effort (offspring birth weight  $^{0.75}$ /maternal weight  $^{0.75}$ ) limits differential maternal



expenditure in ungulates. Our calculated level of reproductive effort for guanacos falls within the range of those species showing no differential maternal expenditure on offspring. The models of Trivers and Willard (1973) and Maynard-Smith (1980) have not been supported in many cases. Even in studies which seemingly support these models, the ultimate causes of differential maternal expenditure on sons and daughters are not clear.

It also appears that juveniles can increase their time in family groups, hence extending the period of parental care, by employing greater than average frequencies of submissive behavior. Additionally, because of the general timing of expulsion, juvenile females remain in family groups longer than juvenile males and have a longer period of parental care than juvenile males. Greater parental care may ultimately increase survival and reproductive success. The timing and restricted duration of the expulsion of the majority of yearlings (13 months old) is most intriguing. Most yearlings are expelled shortly after the peak of the mating period. Perhaps it is in the reproductive interest of territorial males to allow juveniles access to territories until after they have mated with their mothers. Additionally, feeding competition in family groups at this point is likely most intense because young chulengos (2-4 weeks old) begin feeding regularly. Is it a coincidence that most of the yearlings are

expelled when many chulengos begin feeding? Yearling expulsion may ultimately be driven by limiting food resources, which would support Dobson's (1982) competition for environmental resource hypothesis.

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