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Allosuckling allows growing offspring to compensate for insufficient maternal milk in farmed guanacos (*Lama guanicoe*)

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ABSTRACT

While allonursing, the provision of milk to non-offspring by females, involves a potential cost to their own offspring, allosuckling, the suckling from females other than their own mother may allow offspring to compensate for previous deficiencies in maternal milk. We tested this hypothesis in farmed guanacos. Under the compensation hypothesis we predicted that mothers of calves exhibiting allosuckling should be in poorer physical condition and should exhibit relatively low acceptance rates to filial sucking attempts compared to mothers whose calf did not allosuckle. We also predicted that calves exhibiting frequent allosuckling should show similar or greater rates of gain in body weight, but similar total (or final) weight in the long term than calves that nursed from their mothers exclusively. We examined the potential effects of sex and order of birth dates of calves on allosuckling, and the effect of female success during agonistic encounters with other females on allonursing. Two stable groups of 15 and 14 mother–offspring pairs of farmed guanacos were studied from birth to approximately 3 months of age. Allosuckling events comprised 5.7% of all suckling events. Allonursing was performed by 52% of dams and 62% of calves exhibited allosuckling. We found similar gain rates in body weight and total weight at 60 days of age between allosuckling calves and filial sucking calves, irrespective of whether their mothers allonursed or not ($P > 0.1$). Body weight of mothers whose calf allosuckled was significantly lower than that of mothers whose calves nursed from them exclusively ($P = 0.02$). In addition, the percentage of acceptance of filial suckling bouts was significantly lower for allosuckling calves ($P = 0.004$). There was no correlation between the frequency of allonursing and the success of dams during agonistic encounters ($P > 0.22$). Our findings are consistent with the hypothesis that guanaco calves used allosucking to compensate for previous deficiencies in maternal milk.

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1. Introduction

The nursing of non-filial offspring (hereafter referred to as allonursing) has been reported in several species of ungulates (e.g. Birgersson et al., 1991; Murphey et al., 1995; Cassinello, 1999; Réale et al., 1999; Landete-Castillejos et al., 2000; Bartoš et al., 2001; Víchová and

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Bartoš, 2005; Zapata et al., 2009a,b). Within species, the frequency of allonursing varies considerably among individuals (Murphey et al., 1995; Pélabon et al., 1998; Ekvall, 1998; Drábková et al., 2008). Age (Hass, 1990; Birgersson et al., 1991), social rank (Cassinello, 1999), and individual predisposition to allonurse (e.g. Murphey et al., 1995; Pélabon et al., 1998; Ekvall, 1998; Drábková et al., 2008) account for some of the variation.

Causes of allonursing in ungulates are not well understood (Víchová and Bartoš, 2005), however, one hypothesized benefit to offspring that suckle from females other than their mothers (hereafter referred to as allosuckling) is an increase in weight gain due to improved nutrition (Roulin and Heeb, 1999; Hayes, 2000). Nevertheless, allosuckling in red deer (Bartoš et al., 2001), river buffalo (Paranhos da Costa et al., 2000) and cattle (Víchová and Bartoš, 2005) did not support this. Instead, allosuckling allowed calves to compensate partly for nutritional deficiencies on a daily basis (Landete-Castillejos et al., 2000). Additionally, allosuckling in free-living mouflons is associated with periods of limited food availability and high neonatal mortality (Réale et al., 1999). Taken together, these observations suggest that juvenile ungulates may allosuckle opportunistically to compensate for insufficient milk intake, particularly under harsh environmental conditions.

In our study we tested the hypothesis that farmed juvenile guanacos allosuckle to compensate for insufficient maternal milk. From the point of view of offspring, we tested the prediction that calves exhibiting frequent allosuckling should gain weight at a similar or higher rate but achieve equal final weight compared to offspring that nursed exclusively from their mothers. From the point of view of breeding females, we predicted that mothers of calves exhibiting allosuckling should be in poorer physical condition and should exhibit relatively higher frequencies of rejection (or lower frequencies of acceptance) to filial offspring suckling attempts compared with dams whose calves did not allosuckle. Given that previous studies have supported the influence of sex of calves, order of birth date, and female success during agonistic interactions with other females, we also examined the association of these factors with the occurrence of allonursing.

2. Materials and methods

2.1. Animals and husbandry

We conducted the study in two guanaco farms located in different regions and in different years. Females on these two farms were the second or third generation descendents of animals caught between 1997 and 1999 on the island Tierra del Fuego (52–56°S, 63–75°W). Animals on Farm 1 were studied during the 2004–2005 breeding season at the 'Lote 15' farm (52°41′S and 70°54′W) in southern Chile. Animals on Farm 2 were observed during the 2006–2007 breeding season on 'El Trapiche' farm (32°15′S and 70°56′W) in central Chile. Similar conditions were encountered on both farms, which included equal availability of space (i.e., 5 ha average paddock size for each family group, see below) and feed (approximately 1 tonne dry matter/ha/year). Alfalfa was provided when natural forage was scarce. The precise genetic relationship between subjects was unknown in both farms at the beginning of the study and is currently being investigated.

Farm 1 had approximately 150 captive guanacos housed in 100 ha site. Despite the existence of 80 multiparous females, only 20 females gave birth to a single calf. From the 20 mother–calf pairs, 15 mother–calf pairs were successfully monitored. The 15 pairs were located in three different paddocks with six, five and four pairs, respectively, including one dominant male and a number of non breeding females resembling natural family groups. Farm 2 consisted of approximately 200 guanacos in an area of 145 ha. Of the 17 multiparous females that gave birth we successfully monitored 14 mother–calf pairs. Similar to Farm 1, mother–calf pairs in Farm 2 were distributed in different paddocks in two groups of nine and five pairs along with a dominant male. Births were concentrated in December and January in both farms. In Farm 1 the eldest calf followed was born on December 15 and the youngest January 13. In Farm 2 the first calf monitored was born on December 11 and the last on January 16. Mother–calf pairs, confirmed by DNA analysis (Zapata et al., in prep.), were individually marked within 48 h of parturition with the same colored cloth collar to facilitate identification.

2.2. Behavioral definitions and measurements

Behavioral observations were conducted between 9:00 and 18:00 h based on Garay et al. (1995). This is the time period during which most suckling bouts occur. Behavioral observations at Farm 1 were conducted from 26 December 2004 to 3 March 2005 for a total of 215 h during 42 days. On Farm 2 animals were observed from 19 December 2006 to 8 March 2007 for 131 h during 31 days. When behavioral observation started, there were animals already born. We successfully followed the animals for which the mother was identified and the birth date was recorded. Observations were conducted by three or four trained observers inside paddocks, using 8×40 binoculars to confirm nipple attachment by calves. Observations were restricted to the first 3 months after calving, which is the most critical time for subsequent survival and reproductive success of both offspring and mothers (Garay et al., 1995; Sarno and Franklin, 1999; Riek and Gerken, 2007). Since there was a time interval of approximately 5 weeks from the birth of the first calf to the birth of the last calf, late born calves were observed for only 2 months.

Suckling duration was measured using a stopwatch. All suckling events lasting >30 s were recorded as suckling bouts; nursing events that lasted less than 30 s were difficult to quantify accurately and were only counted to measure the occurrence and type of suckling (see below). Whenever a calf interrupted a suckling bout for less than 1 min and then continued with the behavior, we considered a single suckling event to have occurred, and the time the calf was not sucking the nipple was subtracted from the suckling bout duration. We recorded calf rejection whenever a mother walked away, spit, or kicked at the calf when it attempted to nurse.

We used the term 'nursing' in reference to the behavior of the mother and 'suckling' to that of calves. Suckling bouts were labeled as 'filial' (F) if a calf was sucking its own mother or 'non-filial' (NF) if a calf sucked an alien mother (after Murphey et al., 1995). The type of nursing bout was categorized as maternal (M) if the mother nursed her own calf or non-maternal (NM) when the mother nursed non-filial offspring. For each suckling bout we recorded the identity of females and offspring, the type of suckling (F or NF), and the type, duration and number of nursing bouts.

Body weight of calves was measured using a hanging scale (Neta® to ± 0.25 kg). Body weight of mothers could not be measured directly. Instead, we estimated body weight from the thoracic girth (TG), a statistical predictor of body weight in guanacos (R^2 = 0.95, Bas et al., 1999). We assigned each female body condition score (BCS). While qualitative, this measure is considered an appropriate indicator of nutritional status (Morand-Fehr et al., 1987). We adjusted the scoring system, previously used for sheep (Russel, 1991) and llamas (Rigalt et al., 2006) to score guanaco females from 1 (thin) to 5 (obese). All measurements were recorded at least three times (evenly distributed over the course of the study) for every female (from the birth of calves until 3 months after calving). Daily weight gain (WG) was estimated as the difference between two measurements and divided by the number of days passed between each measurement. Because calves were growing in a variable social environment, the 'order of birth date' within each group was considered in the analysis. On Farm 2 the order of birth date included 1–9 and 1–5 for groups 1 and 2, respectively. Given that weight at birth could not be measured in all cases this variable was not included in the present study. The effect on body weight (BW) of calves in long term was estimated at 60 days of age. We used the weight at that age, because all animals studied at least reached that age.

2.3. Female success during agonistic interactions

Behavioral interactions were studied in one family group on Farm 1. This family group included one adult male, two adult non breeding females and six breeding females and their calves. The original family group was established during 1998 from one male and three females to which new females were added during subsequent years. Yearlings (guanacos approximately 1-year-old) are then removed before calving time each year in order to avoid aggression by dominant males (Franklin, 1983).

A total of 176 h of observations representing 18 days were used to quantify social interactions between the females. Observations were conducted from 9:00 to 12:00 h, and 14:00 to 18:00 h. During every agonistic interaction we identified the initiator and the resulting winner. Agonistic interactions consisted of (1) postural threatening displays (ears and tail positions, neck and arm movements), (2) front and lateral stroke, kicking, biting, spitting, chasing, chest-ramming, pinning, neck-wrestling, and (3) vocalizations such as snorting, grumbling threat, clicking, screaming, and screeching (Franklin, 1982). Agonistic interactions were utilized to calculate an overall index of female agonistic success (AS) during these interactions as:

$$\mathrm{AS} = \frac{w - l}{t},$$

where w represent the number of confrontations won, l represents the number of confrontations lost, and t represents the total number of encounters (Soto-Gamboa, 2005). We used the 18 days of observations to calculate an average AS for each female. This index ranged between −1 and 1: AS close to −1 indicates an unsuccessful animal that generally lost most agonistic interactions; AS close to 1 indicated a more successful female that generally won most interactions.

2.4. Statistical analysis

Prior to data analysis, the assumptions of normality and homogeneity of variance were examined with the Kolmogorov–Smirnov and Levene's tests, respectively. Whenever these assumptions were not met, we either used parametric tests on transformed data, or used non parametric statistics on the original, untransformed data (Lenher, 1999). Mean duration of maternal (M) and non-maternal (NM) nursing bouts were compared using the paired Student's t-test. Dependent variables were mean body weight gain (WG) and body weight (BW) at 60 days of age. To avoid excessive loss of statistical power due to the simultaneous examination of multiple factors, a preliminary analysis was conducted to identify the statistically relevant factors to be used during a final analysis. First, the effects of 'Farm' and 'Sex of calves' on WG and BW were assessed using the general linear model procedure (GLM) for unbalanced ANOVA, with 'order of birth date' entered as a covariate. After that, the percentage of allosuckling and allonursing arcsine-square root transformed were subsequently entered in the model as covariates.

The percentage of calf acceptance by females was calculated from the total number of rejections and acceptances of suckling attempts, and then arcsine-square root transformed. We then used ANOVA to examine the influence of calf sucking behavior (i.e., filial vs. non-filial sucking calves) on the transformed data.

Spearman's Rho correlation was used to examine associations between the percentage of allosuckling or allonursing and mean WG and BW. We used the 18 days of observations to calculate a single AS per female. We then used the Sperman's Rho coefficient of correlation to examine a relationship between the average AS and the percentage of allonursing behavior per female. All analyses were conducted using the SPSS statistical software, version 11.5 (SPSS Inc., Chicago, IL, USA). All results are shown as mean ± standard deviation (SD).

3. Results

Five female and 10 male calves were born on Farm 1; six female and eight male calves were born on Farm 2. No dead or abandoned calves were recorded, and adoption was not observed. A total of 716 suckling bouts and 177 unsuccessful suckling attempts were recorded on Farm

1. Fifty out of 716 (7%) suckling bouts were NF and 42 out of 177 (24%) unsuccessful suckling attempts were NF. On Farm 2, a total of 966 and 289 suckling bouts and unsuccessful suckling attempts were recorded, respectively. Thirty-four out of 966 (4%) were NF suckling bouts and 55 out of 289 (19%) were NF suckling attempts. On Farm 1, six out of 15 females performed allonursing (40%), and nine out of 15 (60%) calves performed allosuckling. On Farm 2, nine out 14 females (64.3%) allonursed and 10 out of 14 (71.4%) were allosuckling calves. Allonursing varied widely across females on Farm 1. Excluding cases in which allonursing did not occur, the percentage of NM nursing bouts by each female ranged from 1.1% to 26.5% and NF suckling bouts ranged between 1.3% and 28.6% across all suckling occurrences (Table 1). Inter-individual variation seemed lower at Farm 2. The percentage of NM nursing events ranged from 1.1% to 13.6% of nursing bouts, and NF suckling bouts ranged from 1.3% to 23.8% across all suckling occurrences (Table 2).

Duration of maternal nursing bouts was not statistically different from non-maternal nursing bouts in either farm (Farm 1: 1.7 ± 0.14 and 1.5 ± 0.54 min, respectively, $t_{(6)} = -0.715$, $P > 0.1$; Farm 2: 2.0 ± 0.23 and 2.1 ± 0.80 min, $t_{(8)} = 0.332$, $P > 0.1$).

'Farm' and 'sex of calves did not have a significant effect on WG (Farm: $F_{(1,24)} = 2.4$, $P > 0.1$; Sex: $F_{(1,24)} = 1.4$, $P > 0.1$) or on BW (Farm: $F_{(1,24)} = 0.2$, $P > 0.1$; Sex: $F_{(1,24)} = 0.008$, $P > 0.1$). Upon excluding 'farm' and 'sex', BW and WG were predicted using a multiple regression analysis in which the arcsine-square root transformed percentage of allonursing and allosuckling and 'order of birth date' were entered as predictors. Neither of these two models were statistically significant (BW: $F_{(3,25)} = 2.8$, $P = 0.058$; WG: $F_{(3,25)} = 0.44$, $P > 0.1$).

The effect of 'farm' and 'order of birth date' had no effect on TG of dams. In contrast, dams whose calves allosuckled had significantly lower TG, suggesting that they also had lower body weight (F: TG = 115.2 ± 6.1 cm vs. NF: TG = 110.1 ± 3.88 cm; $F_{(1,24)} = 6.67$, $P = 0.02$, Table 3). Given that BCS was assessed only on Farm 2, the relationship between the type of suckling (F vs. NF) and BCS was examined on this farm exclusively. We found that whether offspring exhibit allosuckling or not was not influenced by BCS of their mothers ($F_{(1,11)} = 0.53$, $P > 0.1$).

Overall, the transformed percentage of acceptance of filial suckling bouts was lower for allosuckling calves compared with exclusively filial sucking offspring ($F_{(1,25)} = 10.0$, $P = 0.004$). Given that 'farm' had a significant effect on this measure ($F_{(1,25)} = 7.8$, $P = 0.010$), we also analyzed this variable for each farm separately. While the transformed percentage of acceptance of suckling attempts was lower in NF calves on both farms, this difference reached statistical significance on Farm 1 only (Farm 1: $F_{(1,13)} = 8.3$, $P = 0.013$; Farm 2: $F_{(1,12)} = 2.14$, $P > 0.1$; Fig. 1).

Regarding the success of mothers during agonistic interactions, a total of 597 interactions were recorded. The number of interactions varied across individual females: yellow = 89, blue = 63, white = 140, red = 93, pink = 115, green = 97. AS was not correlated with the 'type of nursing' ($r_s = -0.587$, $P > 0.220$). Intriguingly, however, the most successful female nursed its own calf exclusively. In contrast, one of the two least successful females (9034) exhibited relatively high frequencies of allonursing (24.4% of nursing bouts).

4. Discussion

4.1. Allosuckling and allonursing in guanacos

The percentage of females that allonursed was relatively high in both farms, 40% in Farm 1 and 60% in Farm 2, figures similar to that reported in river buffalo (Murphey et al., 1995), but lower than that recorded in bighorn sheep (89%, Hass, 1990), free-ranging fallow deer (81%, Ekvall, 1998) or captive fallow deer in which all females nursed alien calves (Birgersson et al., 1991; Pélabon et al., 1998).

Guanaco females that allonursed with relatively high frequency during our study were consistently the same individuals, a pattern that mirrors allonursing in river buffalo (Murphey et al., 1995), Saharan arrui (Cassinello, 1999) and red deer (Drábková et al., 2008). Clearly, more research is needed to understand these individual differences (Drábková et al., 2008). Regarding proximate causation, differences in disposition may play a role and make some females especially tolerant of alien offspring (Murphey et al., 1995). From a functional perspective, some females may allonurse non-filial, but still closely related offspring (Roulin, 2002).

Regarding guanaco calves, allosuckling occurred at a relatively high frequency: the percentage of calves that allosuckled was high and similar in both farms (approximately 60%). Similar to dams, calves that allosuckled were usually the same individuals. Moreover, both frequent and occasional allosucklers were consistent in terms of which female they approached to allosuckle, a behavior similar to that reported in piglets (Olsen et al., 1998). The hypothesis that calves learn which females are especially tolerant (or less aggressive) to non-offspring (Olsen et al., 1998) needs to be examined.

4.2. Growth compensation through allosuckling

Our study provided support to the compensation hypothesis as an explanation to allosuckling in farmed guanaco calves. As predicted, daily weight gains and body weight at 60 days of age of calves were not related to the percentage of allosuckling and allonursing. Secondly, mothers whose calf allosuckled exhibited significantly lower body weight and acceptance of nursing attempts from filial calves than mothers whose calves nursed from them exclusively. Similar support has been found in water buffalo (Murphey et al., 1995; Paranhos da Costa et al., 2000), red deer (Bartoš et al., 2001), and beef cattle (Víchová and Bartoš, 2005). For instance, allosuckling by calves is correlated with relatively low growing rates and low weaning weight in red deer (Bartoš et al., 2001). In Iberian red deer, the frequency of allosuckling increases after the time maximum milk production, suggesting that allosuckling is a response to compensate for a reduced maternal milk supply (Landete-Castillejos et al., 2000). Altogether, these findings suggest that calves may, to

Table 1
Frequency of allonursing and allosuckling bouts on Farm 1. Column 'Mothers' indicates female's identification which performed allonursing to a given calf assorted on the first line. Calves are grouped by paddock where they stayed during the study. Spaces with horizontal lines are used to denote filial nursing.

Group	Mother ID	Calf ID															NF nursing bouts	NF nursing bouts (%)
		Total nursing bouts (F + NF)	11-4	7-4	5-4	6-4	9-4	8-4	14-4	12-4	13-4	15-4	10-4	16-4	1-4	2-4	3-4	
1	H-1	41	–	6	4	0												10	24.4
	122	14	0	–	0	0												0	0
	A01	20	0	0	–	0												0	0
	12	25	0	0	0	–												0	0
2	9034	136					–	16	1	4	15	0						36	26.5
	9140	66					0	–	0	0	1	1						2	3.0
	126	79					0	0	–	0	0	0						0	0
	Fuchsia	92					1	0	0	–	0	0						1	1.1
	2007	67					0	0	0	0	–	0						0	0
	118	30					1	0	0	0	1	–						2	6.7
3	809	29											–	0	0	0	0	0	0
	154	32											0	–	0	0	0	0	0
	128	22											0	0	–	0	1	1	4.5
	60-7	17											0	0	0	–	0	0	0
	806	13											0	0	0	0	–	0	0
		NF suckling bouts	0	6	4	0	2	16	1	4	15	1	0	0	0	0	1	56	
		Total suckling bouts (F + NF)	41	21	24	25	99	76	80	97	83	29	29	32	21	17	14		
		NF suckling bouts (%)	0	28.6	17	0	2	21.1	1.3	4.1	18.1	3	0	0	0	0	2		

Table 2
Matrix of allonursing and allosuckling on Farm 2. Column 'Mothers' indicates female's identification which performed allonursing to a given calf assorted on the first line. Calves are grouped by paddock where they stayed during the study.

Groups	Mother ID	Calf ID														NF nursing bouts	NF nursing (%)
		Total nursing bouts (F + NF)	Dark red	Orange	Red and black	Pink	Violet	Fuchsia	Pink	Green	Striped	Blue	Yellow	White	Light blue	Red		
1	Dark red	72	–	2	2	2	0										6	8.3
	Orange	57	0	–	0	0	0										0	0
	Red and black	72	0	0	–	0	0										0	0
	Pink	72	1	0	0	–	0										1	1.4
	Violet	50	0	0	0	0	–										0	0
2	Fuchsia	72						–	0	0	0	0	1	0	5	2	8	11.1
	Pink	79						1	–	0	0	0	1	0	0	0	2	2.5
	Green	59						0	0	–	0	0	0	0	0	0	0	0
	Striped	40						0	0	0	–	0	0	0	0	0	0	0
	Blue	109						5	1	0	0	–	0	0	0	0	6	4.6
	Yellow	93						1	0	0	0	0	–	0	0	0	1	1.1
	White	88						9	0	0	0	0	3	–	0	0	12	13.6
	Light blue	62						3	0	0	0	0	0	1	–	0	4	6.5
	Red	41						1	0	0	0	0	0	0	0	–	1	2.4
		NF suckling bouts	1	2	2	2	0	20	1	0	0	0	5	1	5	2	41	
		Total suckling bouts (F + NF)	67	59	74	73	50	84	78	59	40	103	97	77	58	42	41	
		NF suckling bouts (%)	1.5	3.4	2.7	2.7	0	23.8	1.3	0	0	0	5.2	1.3	8.6	4.8		

Table 3
Analyses of variance. Dependent variable: 'thoracic girth'; factors: 'farm' and 'type of suckling' of calves (F vs. NF); 'order of birth date' was used as covariate.

Source	Type III sum of squares	df	Mean square	F	P
Corrected model	268.7[a]	4	67.2	3.02	0.04
Intercept	80,381.1	1	80,381.1	3613.75	<0.01
Order of birth date	22.8	1	22.8	1.02	>0.1
Farm	26.4	1	26.4	1.18	>0.1
Type of suckling	148.4	1	148.4	6.67	0.02
Farm*type of suckling	40.2	1	40.2	1.81	>0.1
Error	533.8	24	22.2		
Total	365,004.2	29			
Corrected total	802.5	28			

[a] $R^2 = 0.34$.

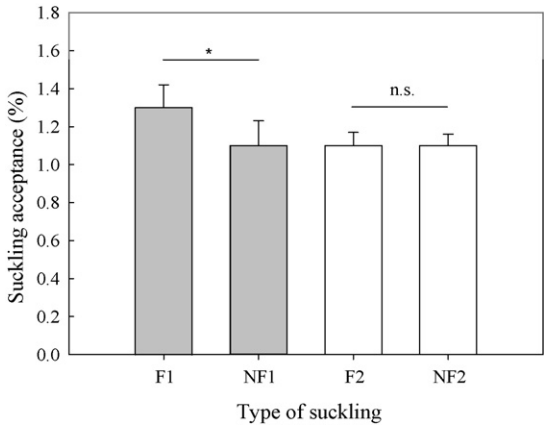

Fig. 1. Arcsine-square root transformed percentage of suckling acceptance on Farm 1 (grey bars and "1" subscript numbering) and Farm 2 (white bars and "2" subscript numbering), for filial (F) and non-filial (NF) suckling. The asterisk indicates statistically significant differences within farm at $P < 0.05$; n.s. indicates a statistically non significant difference.

varying extents, compensate deficiencies in maternal milk supply through allosuckling. Subsequent studies are needed to examine whether quality and quantity of milk supplied by maternal and non-maternal suckling differ.

4.3. Factors associated to allosuckling and allonursing

Allosuckling was not related to sex of offspring, and offspring sex did not influence daily growth or body weight at 60 days. These findings contrast with that reported in water buffalo where male calves exhibit greater weight gains and spend more time suckling dams other than their own mother compared with female calves (Paranhos da Costa et al., 2000). Whether our findings reflect similar costs and benefits to allosuckling male and female guanacos need to be examined. Contrary to what has been noted in deer (Ekvall, 1998), allonursing by guanaco females was not related to agonistic behavior.

5. Conclusions

Our results suggest that juvenile guanacos perform allosuckling to compensate for previous nutritional deficiencies. Dams whose calves performed allosuckling exhibited poorer body condition and less percentage of acceptances of filial suckling bouts compared to dams that nursed their offspring exclusively. Both measures are indirect indicators of poor maternal milk supplied. Therefore, our findings are consistent with the hypothesis that guanaco calves use allosuckling to compensate for previous deficiencies in nourishment.

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