Allonursing in Captive Guanacos, *Lama guanicoe*: Milk Theft or Misdirected Parental Care?

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Abstract

Females in several ungulates transfer milk to non-filial (NF) offspring, in a process known as allonursing. This behavior is less common in monotocous species, including most ungulates, and it has been associated with parasitic behavior of calves or mothers who have lost their own offspring. To examine whether the calves 'steal' milk from the females or whether females fail to discriminate their own calves in guanacos, allonursing behavior was observed. If milk theft drives allonursing, mothers should reject NF offspring, they should search for their own calves, and calves attempting to suckle from alien mothers should adopt parallel (as opposed to the anti-parallel) position during allonursing. Alternatively, if allonursing is caused by mothers unable to discriminate own offspring, mothers are not expected to reject NF offspring, and alien calves should use parallel and antiparallel position similarly when allonursing. Allonursing was investigated during the first 3 mo of lactation in two groups of captive guanacos composed of 15 and 14 mother-calf pairs, respectively. While 40% and 62.5% of mothers in groups 1 and 2 performed allonursing, high individual variation prevailed; some females exhibited this behavior infrequently (4.1% and 6.5 % in groups 1 and 2). The rejection rate to NF nursing attempts was threefold higher than the rejection rate to filial nursing attempts. The occurrence of nursing to NF was associated to a parallel posture by the calves. Our findings suggest that 'milk theft' is a more plausible hypothesis to explain allonursing in guanacos than 'misdirected parental care'.

Introduction

Allonursing or non-offspring nursing refers to females allowing alien offspring to suckle (Packer et al. 1992; Murphey et al. 1995), and represents one extreme case of alloparental care (Riedman 1982). Allonursing has been reported in 68 mammalian species (Packer et al. 1992), and is a puzzling behavior. Lactation is the most energetically expensive behavior of mammals (Gittleman & Thompson 1988) and lactating females may pay a fitness cost in terms of subsequent survival and reproductive success (Clutton-Brock et al. 1989). The transfer of milk or any other form of parental care to unrelated offspring by a female could reduce the amount of nutrients available to her current young or increase the transmission of internal and external pathogens to her (Roulin & Heeb 1999).

Both adaptive and non-adaptive hypotheses have been proposed to explain the evolution of allonursing under natural conditions (Hayes 2000; Roulin 2002). Allonursing can provide indirect fitness

benefits if restricted to close kin (e.g. prairie dogs, *Cynomys ludovicianus*, Hoogland et al. 1988). Females can also reciprocate during allonursing and provide milk to each other's offspring, which decreases temporal variation in their ability to produce milk (e.g. lions: Pusey & Packer 1994). Alternatively, allonursing may represent a non-adaptive by-product of communal rearing that results from milk theft by the young (e.g. river buffalo: Murphey et al. 1995) or misdirected maternal care due to overcrowded conditions (e.g. seals: Boness 1990).

While allonursing has been reported in numerous species from a wide range of mammalian orders (Packer et al. 1992), the extent of this behavior varies greatly among taxa. In monotocous taxa (i.e. with a litter size of one offspring), including most ungulates, allonursing is less common than in polytocous taxa. Allonursing was reported in 15 of 30 species of ungulates examined by Packer et al. (1992). More recently, other ungulate species have been added to this list, including fallow deer (*Dama dama*, Ekvall 1998), river buffalo (*Bubalis bubalis*, Murphey et al. 1995), wild mouflon (*Ovis musimon*, Réale et al. 1999), domestic South American camelids (Brown 2000) and bighorn sheep (*Ovis canadensis canadensis*, Hass 1990). While these studies have assessed the extent of allonursing across species, few have tested hypotheses that could elucidate the evolution of allonursing in ungulates (e.g. Murphey et al. 1995; Pélabon et al. 1998; Landete-Castillejos et al. 2000; Bartoš et al. 2001; Víchová & Bartoš 2005). The seminal article of Packer et al. (1992) found allonursing in ungulates to be associated with high levels of 'milk theft' by parasitic infants, and to be more common in species where females continue to nurse after they have lost their own young. Similar findings were reported in river buffalo (Murphey et al. 1995), but not in other ungulates such as the Saharan arrui, *Ammostragus lervis* (Cassinello 1999), where misdirected parental care seems to explain allonursing better. Another common explanation is inclusive fitness benefits when mothers allonurse to close kin (Roulin 2002), however this hyphotesis has been little explored in ungulates (Walt et al. 1995; Cassinello 1999).

Among South American camelids, allonursing has been observed in free ranging (Zapata et al. 2009) and captive guanacos (Zapata et al. 2006). Guanacos are monotocous, highly social, monomorphic animals that exhibit a resource defense polygyny mating system (Franklin 1983). Territorial and migratory populations have been described for this species (Franklin 1983; González et al. 2006). Reproductive units or family groups include one adult male and several breeding females and their offspring (Sarno & Franklin 1999). Family groups remain together from September to March. Birth occurs in November and December after an 11.5-mo gestation (Ortega & Franklin 1995). Male and female calves are expelled by the male when they are about 1 year old (Sarno et al. 2003).

The function of allonursing remains unclear in this species, and no functional studies are available on South American camelids. The aim of this study was to examine two hypotheses explaining allonursing in ungulates in captive guanacos which have been supported in ungulates (Packer et al. 1992): the parasitic behavior of the calves (milk theft hypothesis), and the misdirected parental care hypotheses. According to the parasitic hypothesis, (1) mothers should actively reject non-filial (NF) offspring, and (2) NF calves should often use a parallel (as opposed to an antiparallel) position when attempting to suckle. The parallel position is thought to prevent females from recognize and discriminate their own young (Bartoš et al. 2001). According to the misdirected parental hypothesis, (1) mothers are not expected to reject (i.e. discriminate) NF offspring, and (2) NF calves should use parallel and antiparallel position similarly when allonursing. In addition, we recorded the response of mothers to the approach to their own vs. an NF calf after a brief separation. Olfaction of the ano-genital region facilitates mother-offspring recognition in red deer (Bartoš et al. 2001). To test these predictions, we studied the nursing behavior of two groups of captive guanacos during the first 3 mo postpartum, a time period that is critical for the subsequent survival and reproductive success of both offspring and mothers in this species (Garay et al. 1995; Sarno et al. 1999; Riek & Gerken 2007).

Materials and Methods

Study Subjects and Animal Husbandry

Two groups of captive guanacos were studied. Females in these groups were the second or third generation descendents of animals caught between 1997 and 1999 at Tierra del Fuego Island (52° and 56°S, and 63° and 75°W) (Bas & González 2000). Group 1 was studied during the 2004–2005 breeding season at the Lote 15 farm (52°41'S and 70°54'W) in southern Chile and Group 2 was examined during the 2006–2007 breeding season at the El Trapiche farm (32°15'S and 70°56'W), central Chile. Both study groups were housed under similar conditions

of overall space available (i.e. 5 ha average paddock size), and had a natural pasture-based feeding regime (approximately 1 ton dry matter/ha/yr) and alfalfa hay was offered when the natural forage is scarce. The precise genetic relationships among subjects were unknown on both farms.

The group at Lote 15, hereafter referred as Farm 1, had approximately 150 captive guanacos housed on 100 ha. A total of 20 multiparous females gave birth to a single calf in this group. Fifteen of these 20 mother-calf pairs were successfully marked and monitored. At El Trapiche guanaco farm, hereafter referred as Farm 2, the population size was approximately 200 guanacos housed on 143 ha. Seventeen multiparous females gave birth in this group, and 14 mother-calf pairs were successfully marked and studied. Mother-calf pairs were marked with the same colored cloth collar to facilitate identification. Mother-calf pairs were individually marked within 48 h of parturition.

Behavioral Observations

Behavioral observations were conducted between 9:00 and 18:00 h which is, the time period during which most suckling bouts occur in wild guanacos (Garay et al. 1995). Behavioral observations at Farm 1 were conducted from 26 December 2004 to 3 March 2005 for a total of 215 h over 42 d. At Farm 2, animals were observed from 19 December 2006 to 8 March 2007 for 131 h over 31 d. Observations were conducted by 3–4 trained observers inside paddocks, at a distance of 5–10 m from the animals, all of which were habituated to the human presence. We used 8 × 40 binoculars to confirm nipple attachment by the calves.

All nursing events lasting 30 s or more were recorded as nursing bouts; nursing events that lasted <30 s were more difficult to quantify accurately and were counted only into the suckling frequency estimates. Nursing bouts were labeled as 'filial' (F) if a mother was nursing her own calf or 'non-filial' (NF) if a mother nursed an alien calf. Mothers nursing F and NF calves simultaneously were scored as F + NF; females nursing more than two calves at the same time we recorded as F + NF + Nº extra calves. The body posture adopted by the calf during suckling was scored as antiparallel when the head of the calf was located in opposite direction to the head of the mother, perpendicular when the body of the calf pointed towards one side of the mother, and parallel when the head and body of the calf were located towards the head of the mother. The response of mothers when approached by F or NF calves was scored on a scale of increasing 'awareness': feeding, standing, ear movements, the head is turned back, the calf is sniffed. Whenever a mother exhibited two behavioral units along this scale, we recorded the highest as the response. Every time a female walked away from, kicked or spit to (from) an F or NF calf that approached her, we scored her as rejecting the young. We calculated a rate of rejection to F calves as the number of rejections to F/the number of acceptances to F nursing attempts; a rejection rate for NF calves was calculated as rejections to NF/acceptances to NF. These ratios were calculated as an indirect measure of calf discrimination by the females.

Data Analysis

Data from different farm groups were examined separately because they involved different groups of animals and were studied during different years. Variables expressed as percentages were arsine-square root transformed before statistical analyses and 0.5 was added to all data whenever zeros were present (Lehner 1998). The assumptions of normality and homogeneity of variances were examined with the use of Kolmogorov-Smirnov's test and Levene's tests, respectively (Lehner 1998). All variables used were discrete (1 presence; 0 absence) and statistical analyses were performed over frequencies. We used the paired Student's t-tests to compare the arsine square root percentages of NF and F nursing, and rejection rate to F vs. rejection rate to NF nursing attempts, and the transformed proportion of

Table 1: Frequency of filial (F) and non-filial (NF) nursing bouts in captive guanacos

Group	Suckling bout	Frequency	%
Farm 1	F	633	93.5
	NF	12	1.8
	F + NF[a]	26	3.8
	F + NF × 2[b]	5	0.7
	F + NF × 3[c]	1	0.2
	Total	677	
Farm 2	F	929	95.9
	NF	33	3.4
	F + NF[a]	7	0.7
	F + NF × 2[b]	0	0.0
	F + NF × 3[c]	0	0.0
	Total	969	

[a]Suckling bout includes filial calf and one alien calf.
[b]Suckling bout includes filial calf and two alien calves.
[c]Suckling bout includes filial calf and three more alien calves.

Table 2: Mean proportion of rejection/acceptations filial (F) or non-filial (NF) nursing bouts ± SEM in captive female guanacos

	Rejection to filial/acceptance to filial	Rejection to NF/acceptance to NF	t-value	df	p-value
Farm 1	0.14 ± 0.031	0.39 ± 0.34	−2.70	14	0.016
Farm 2	0.23 ± 0.020	0.63 ± 0.10	−3.72	13	0.003

Table 3: Parameters of statistically significant equations obtained during binary logistic regressions to predict filial (F) or non-filial (NF) nursing, the dependent variable

	B ± SE	Wald	df	p-value
Farm 1				
Parallel[a]	−1.30 ± 0.462	7.191	1	0.007
Standing[a]	−1.30 ± 0.350	13.492	1	<0.001
Farm 2				
Parallel[a]	−1.02 ± 0.415	6.041	1	0.014
Standing[a]	−1.28 ± 0.414	9.514	1	0.002

Independent variables were nursing posture and mother's response to calves that approching her to nurse. Nursing postures were antiparallel, parallel and perpendicular (0 present; 1 absent), and mother responses included feeding, standing, ear movement, turning its head back, and sniffing the calves (0 present; 1 absent).
[a]Variables entered on the step 3 followed a conditional entering of variables in the regression.

allosuckling between early and late lactation. We also used Student's t-tests to examine whether the proportion of allosuckling differed between early and late lactation. 'Early lactation' included observations recorded from birth until four weeks of lactation, and 'late lactation' included observations recorded from week 5 until the end of the study period (based on Riek & Gerken 2007). The Wilcoxon signed rank test was used to compare the responses of mothers to F or NF calf approaches. A binary logistic regression was conducted to predict F or NF nursing. The variables tested were nursing posture (antiparallel, perpendicular or parallel) and mother response (feeding, standing, ear movement, turning its head back and sniffing). Variables were entered using the conditional modality. All analyses were conducted using SPSS statistical software, version 11.5 (SPSS Inc., Chicago, IL, USA).

Results

Six of 15 females (40%) at Farm 1 and nine of 14 females (62.3%) at Farm 2 exhibited allonursing (Table 1). At Farm 1, 6.5 % of nursing bouts were NF and at Farm 2, 4.1% of nursing bouts were NF. The mean percentage of F nursing was significantly greater than NF nursing at Farm 1 ($\bar{x}$ ± SEM: 95.9 ± 2.19% vs. 4.01 ± 2.19%; $t_{(14)} = 14.26$, $p < 0.001$), and Farm 2 ($\bar{x}$ ± SEM: 96.9 ± 1.03% vs. 3.08 ± 1.03%; $t_{(13)} = 14.09$, $p < 0.001$).

The most frequent type of NF nursing in Farm 1 was F + NF (59%), followed by NF (27.3 %), and nursing that involved more than one alien calf simultaneously (13.7% Table 2). In Farm 2, NF nursing involved a single alien calf (82.5%) and no nursing of multiple NF calves were ever observed. It is worthy to mention that in Farm 2, most of these NF nursing bouts were observed while females received alfalfa hay on the ground in a surface of 4 × 10 m.

The time of lactation did not influence the proportion of allosuckling. Allosuckling during early lactation did not differ from that during late lactation at Farm 1 ($t_{(4)} = 0.9$, $p > 0.1$), or Farm 2 ($t_{(5)} = -0.23$, $p > 0.1$). At both farms, the rate of rejection to NF nursing attempts was significantly greater than the rate of rejection to F nursing attempts (Table 2). The rate of rejection to NF nursing attempts was almost threefold greater than the rate of rejection to F nursing attempts in both farms. Upon using a binary

Table 4: Mean percentage (± SE) of mothers' response to the approach of filial (F) vs. non-filial (NF) offspring in captive guanaco females

	Mother response	F	NF	Z	p-value
Farm 1 (n = 15)	Feeding	18.4 ± 3.43	3.7 ± 3.70	−3.296	0.001
	Standing	22.3 ± 3.36	49.4 ± 18.40	−1.420	>0.1
	Ear movement	29.4 ± 4.32	2.2 ± 2.20	−3.410	0.001
	Turn its head back	11.4 ± 1.90	23.6 ± 15.96	−2.329	0.020
	Sniffing	17.9 ± 2.58	21.2 ± 15.99	−2.417	0.016
Farm 2 (n = 14)	Feeding	31.2 ± 8.36	61.0 ± 14.30	−0.659	>0.1
	Standing	19.1 ± 6.00	8.6 ± 5.71	−3.107	0.002
	Ear movement	9.8 ± 4.12	29.2 ± 15.98	−1.350	>0.1
	Turn its head back	7.5 ± 4.37	1.3 ± 1.30	−3.230	0.001
	Sniffing	32.3 ± 7.64	0.0	−2.52	0.012

Statistical comparisons were performed with the use of Wilcoxon signed ranks tests.

logistic regression, the parallel nursing posture and the standing mother response were found to be significant predictors of F vs. NF nursing (Table 3) in both farms, whereas the other nursing postures and mother responses were not found significant predictors of allonursing.

Females at Farm 1 exhibited more feeding and ear movement upon the approach of F than upon the approach of NF calves (Table 4). These females also turned their heads more often and sniffed NF calves more than they did F calves. Females remained in a standing posture when approached by F and NF calves similarly (Table 4). In contrast, females at Farm 2 kept feeding and moved their ears similarly when approached by F and NF calves (Table 4). In addition, females at Farm 2 stood, turned their head, and sniffed F more than NF calves.

Discussion

Allonursing occurred in 4.1% and 6.5 % of nursing bouts in two groups of captive guanacos, respectively. The similar extent of this behavior in both farms may reflect similar housing conditions. In fact, both farms shared similar paddock size, animal density and carrying capacity, food availability and predator control. The extent of allonursing recorded in guanacos is similar to that reported in captive Saharan arrui (3.3%, Cassinello 1999), and in red deer during the first month of life (Drábková et al. 2008), but low compared with other ungulates. For instance, the percentage of allonursing bouts reaches 19% in cattle (Víchová & Bartoš 2005), 23% in captive fallow deer and 41% in free-ranging fallow deer (Birgersson et al. 1991; Ekvall 1998).

Nursing to single NF calves (i.e. when no other calf is present) reached 27% and 82.5% of all nursing events in farms 1 and 2, respectively. This figure tends to be even less common in other ungulates in which allonursing typically involves multiple calves, including the F calf (e.g. fallow deer; Birgersson et al. 1991; Ekvall 1998). Nevertheless, on Farm 2, the nursing of NF calves in the absence of F calves occurred mostly when mothers received alfalfa hay supplementation, and NF calves seemed to take advantage of the lack of attention of the females.

The proportion of allonursing did not increase throughout the lactation period as has been reported in fallow deer (Ekvall 1998) and Iberian red deer (Landete-Castillejos et al. 2000). However, it is possible we failed to detect a shift in the proportion of allonursing during the lactation period in guanacos because our observations focused on the first stage and not on the entire lactation period (i.e. over 1 yr; Garay et al. 1995).

We found that at both farms, the rate of rejection to NF nursing attempts was higher than the rejection to F nursing attempts, implying that females rejected proportionally more NF solicitations than F solicitations, an observation that provides indirect evidence of discrimination against NF calves by the females. In addition, a parallel posture characterized suckling by calves during allonursing. These findings are consistent with the hypothesis that allonursing in guanacos is the result of opportunistic milk theft by the calves rather than the result of misdirected parental care by the mothers.

While mothers are known to allonurse, rejection of NF nursing solicitations is also common in ungulates (Birgersson et al. 1991; Walt et al. 1995; Ekvall 1998; Pélabon et al. 1998; Cassinello 1999; Bartoš et al. 2001). In Saharan arrui and fallow deer, young mothers are more aggressive than older females, and calves learn to avoid them and approach older females more often (Ekvall 1998; Cassinello 1999). It is possible that calves learn how to approach females other than their mother to avoid rejection. Potential tactics may involve approaching of females from behind, and the concentration of nursing attempts whenever the F calf is suckling. In this study, we found that the parallel position adopted by the young was a good predictor of NF nursing as reported in red deer (Bartoš et al. 2001). In cattle, river buffaloes and fallow deer, suckling from a calf's own mother almost exclusively occurs in the normal antiparallel position, whereas alien calves nurse alien females exclusively from behind or while standing in a parallel posture (Spinka & Illman 1992; Murphey et al. 1995; Walt et al. 1995; Ekvall 1998).

Data from this study also suggested that mothers at Farm 1 were more tolerant of NF calves than were mothers at Farm 2. At Farm 1, the proportion of NF rejections was smaller, there were more multiple NF nursing events, and mothers seemed more 'aware' of the approaches of NF calves (turning their heads back and sniffing NF sucking calves). Differences in the behavior of females at both farms in relation to F and NF offspring approaches may be linked to differences in the level of relatedness of females on each farm. Currently, we are conducting molecular analyses to examine this possibility, as it is of course the case that the alternative hypotheses are not mutually exclusive (Roulin 2002).

Could allonursing observed in guanacos be the by-product of captivity? In this study, the provision of milk to NF young did not seem to result from animals being held in a fenced area. Mothers were not observed leaving the group when nursing her young although they had opportunities and space in which to do so. Instead, the herd stayed together and never used the whole paddock area at the same time. Moreover, allonursing was recorded recently in a free-ranging population of guanacos (Zapata et al. 2009), an unusual piece of evidence that has been reported in only half ungulate species in which allonursing has been reported (for a review see Víchová 2003). Thus, the available evidence indicates that allonursing in guanacos occurs naturally, albeit at a low frequency.

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