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SUCKLING BEHAVIOR IN DOMESTIC GOATS: INTERACTION BETWEEN LITTER SIZE AND KID SEX

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ABSTRACT: Studies of milk allocation in polytocous species provide the opportunity to investigate the effects of offspring number and sex ratio on maternal investment. In these species maternal control over milk allocation is more difficult because physiological limits on milk production may stimulate sibling competition. This study investigated the nursing behavior of domestic goats bearing twins or singletons in an experimental situation for the first 47 days post-partum. Milk yield and composition did not correlate with litter size, kid weight, or with the behavior of kids. Males were heavier than females, but there were no sex differences in behaviors related to nursing. Milk allocation differences existed between twins and singletons, even though, on the average, there were no significant weight differences. However, one twin was always larger than the other. Twins spent less time in proximity to the mother than did the singletons, and were more responsible for achieving proximity to the mother. These results suggest that nursing behavior was more affected by litter size than by sex of young, although there might be an interaction between both, that early mother-young interactions were different for twins and singletons, and that kids played an active role in the allocation of milk and its conversion to body weight.

Infant mammals are entirely dependent on milk to meet their nutritional needs during early development; milk consumption is directly related to infant growth, and milk is the conduit for the transfer

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of proteins necessary for the development of an immune system (Jenness, 1986). Therefore, infants and juveniles should strive to acquire as much of this essential resource as possible, and mothers should distribute it in a manner that increases their own reproductive success, both immediate and future (Trivers, 1974; Wilson, 1975). Since the genetic self-interests of mother and offspring are not necessarily congruent (Trivers, 1974), and young differ in reproductive value and needs (Mock & Forbes, 1992), milk allocation provides a rich context for parent-offspring conflict. Studies of parental care have been concerned with how resource allocation to progeny is biased by offspring sex and litter size (Winkler & Wilkinson, 1988), but few studies consider the interaction between both (Gaillard, Pointier, Brandt, Jullich, & Allaine, 1992; Soderquist, 1995).

For polygynous mammals, evolutionary theory predicts that mothers should bias milk allocation toward sons if (1) maternal provisioning is positively related to offspring size at maturity and (2) increased maternal provisioning has a more pronounced effect on the fitness of sons than of daughters (Byers & Bekoff, 1990; Maynard Smith, 1980; Trivers, 1972). This might plausibly occur in species in which adult size is influenced by access to food during early development and in which larger males enjoy a competitive advantage over smaller males in obtaining mates. Although some studies have documented that male offspring receive a greater investment of maternal resources than female offspring (see reviews by Byers & Bekoff, 1990; Clutton-Brock, 1991), Byers and Bekoff (1990) argued that whether the mother or offspring control resource allocation has not been demonstrated adequately. This demonstration is needed to understand the extent to which natural selection operates on maternal and infant traits. A complete understanding of the mechanisms of milk allocation requires investigation of the dynamics of parent-offspring interactions, especially the role of the young in mediating the distribution of milk .

Ungulates present an excellent opportunity to test these theoretical predictions, because they show a wide range of polygyny, sexual dimorphism, and males fight for access to females (Jarman, 1983); and because the young, although precocial in comparison to most other mammals, are dependent on milk for the first three or four months of life. Male-biased milk allocation has been described in bison (*Bison bison*), horses (*Equus caballus*), and red deer (*Cervus elaphus*), but not in cattle (*Bos* sp.), bighorn sheep (*Ovis canadensis*), white tail deer (*Odocoileus virginianus*), and fallow deer (*Dama dama*), for example (reviewed by Byers & Bekoff, 1990; Clutton-Brock, 1991). In some polytocous species, such as pronghorn (*Antilocapra americana*), female offspring seem to suckle more than males (Byers & Moodie, 1990). In species with high growth rates, mothers might be near the upper limits of milk production and may not be able to provide enough extra milk to support differential investment in any one sex (Byers & Moodie, 1990).

Although studies of sex-biased milk allocation in ungulates have focused on species bearing single offspring, polytocous species provide the opportunity to investigate the effects of offspring number and sex ratio on milk allocation. In these species maternal control over milk allocation is more difficult because physiological limits on milk production may stimulate competition between siblings. Reduced suckling frequencies and/or growth rates in twins relative to singletons have been reported in domestic sheep (Ewbank, 1965, 1967) and cattle (Price, Martinez, & Coe, 1984/85), suggesting that sibling competition might be expected. However, the litter size effect was not present in pronghorn antelope for nursing frequency (Byers and Moody, 1990). Since sibling competition can reduce the fitness of parents (Godfray & Parker, 1992), mothers might be expected to buffer sibling interactions (Pianka, 1988) or to favour offspring most likely to increase her inclusive fitness (Maynard Smith, 1980). For example, in the first two hours after parturition, domestic goat mothers provide more nursing to the smaller, less vigorous kid, and these compensation efforts correlate with the dominance status of these kids (Klopfer & Klopfer, 1977; Klopfer & Klopfer, 1973). Thus, studies of milk allocation in polytocous species should consider, in addition to sex-biased milk allocation, the dynamics of nursing several young versus one, and whether the mother buffers or encourages sibling competition. Furthermore, different litter sizes represent different social environments, and thus a context to study alternative behaviors used by the young in the procurement of resources.

In this study we investigated the nursing behavior of domestic goats bearing twins or singletons in an experimental situation for the first 47 days post-partum. Our objectives were to evaluate whether the expected sex-biased milk allocation was evident in either singletons or twin litters, to ascertain the role of the young in the allocation of milk, and to determine the extent to which litter size affects mother-young interactions. Subsidiary goals were to characterize sibling competition and observe whether mothers mediated competitive interactions among siblings. Domestic goats are a particularly appropriate model for studying the dynamics of nursing interactions because they are highly tractable, produce up to four offspring per litter, and mother-young interactions are fairly well characterized. Also, for dairy breeds it is unlikely for differential investment to be limited by milk availability. This provides a convenient context in which to examine the relative roles of mother and infant in controlling access to maternal resources.

METHOD

Subjects

This study was conducted at the Dairy Goat Research Facility of the University of California at Davis. The study group consisted of 18 adult female Alpine-breed goats between 2 and 3 years of age and their 26 offspring. Several subjects were eliminated from the study because of illness, therefore only the behavioral and growth data from 16 does and 22 kids are presented here: 6 sets of twins (4 male-female, 1 male-male, 1 female-female) and 10 singletons (5 males and 5 females). Milk composition data were collected for 16 of the does. All adult goats had given birth once previously, but this was the first time that they were allowed to raise kids. The mean body height at the shoulder for adult does was 72.17 cm (SD=3.38) and the mean body weight was 47.19 kg (SD = 6.89). All subjects were housed in a 33.2 x 7.4 m corral with an elevated wooden shed for shelter. Hay and grain were provided *ad libitum* once a day. The does were allowed to nurse their kids ad libitum during non-test days, but on test-days they were allowed to nurse their kids only during the observation time.

Procedure

The objective was to structure mother-offspring reunions so that we could observe nursing dynamics under conditions in which mother and offspring were motivated to engage in the interaction. The kids were observed at around 5, 12, 19, 26, 33, 40, and 47 days of age. Kids were artificially weaned at 52 days of age. At each age, three observation sessions were done between 7 and 10 am, and three between 7 and 9 pm. Kids were separated from their mothers around 10pm the night before each of the morning observations and around 10:30 am before the afternoon observations. These procedures were not different from normal husbandry procedures at the Dairy Goat facility. These separation times are not unusual for domestic animals and are within the range seen for feral goats (Coblentz, 1974; O'Brien, 1984; Ruiz-Miranda & Chabert, 1989). Because births were not completely synchronous, only between 4 and 6 kids were tested simultaneously.

The focal units were the mother and her one or two kids, and were observed for a minimum of 45 minutes and a maximum of 90 minutes. The time differences depended on the visibility of subjects, and unpredictable environmental factors. Before reintroducing the mothers to the home corral containing the rest of the females and their kids, we confined the kids behind a shed, releasing them only after their mothers entered the corral. All occurrences sampling (Martin & Bateson, 1986) was used to record nursing and approaches and leaves, and 5-minute interval sampling was used to record distance between kid and mother, and the behavior of kids. Behavioral variables analyzed were:

1. *Proximity to the Mother*. The number of intervals spent at distances of 2 meters or less from the mother were grouped under the label "Proximity".

2. *Kid Behavior*. Resting: Lying down alone or with its sibling in a covered area for more than 15 seconds. Feeding: Mouthing or chewing anything that was not milk or part of the corral furniture. Ruminating was also included here. Other: Any behavior that did not fit into one of the preceding categories.

3. *Approaches and Leaves*. We recorded the initiator and frequency of approaches (a distance change from more than 1 meter to within a meter of the target animal), or leaves (move away to a point further than one meter from target animal) between mother and offspring.

4. *Nursing*. A nursing bout (i.e., a nursing event) was defined as the kid suckling for 5 seconds or more with no interruptions longer than 5 seconds. For analysis, the total number of bouts was divided by the total observation time to calculate the Nursing Bout Rate. Bout Length was defined as the mean of the durations of all nursing bouts. Time Nursing was defined as the sum of the durations of all nursing bouts divided by the total observation time. In addition, for each nursing bout we recorded which kid nursed first, which kid was the displacer (see below), and the dam's behavior. A displacer was any kid that approached from the same side as the nursing kid and pushed the nursing kid off the nipple that it was suckling, thereby forcing it to use the other nipple or abandoning nursing completely. The behavior of the dam was recorded as Presentations (any behavior done by the mother that resulted in a kid being closer to the udder as opposed to the face of the mother) or Withdrawals (any behavior that resulted in the kid being

farther away from the udder). Withdrawals and Presentations took the form of licking or butting or walking a few steps or turning around. These behaviors were interpreted to be a solicitation or encouragement to nurse.

6. *Nursing Failures.* Attempts at nursing that were rejected by the mother and were less than 5 seconds long. An attempt to nurse was defined as either touching the udder or getting within six inches from it with the apparent intention to nurse.

6. *Nursing Success.* This was calculated for each kid by dividing the total number of nursing bouts by the sum of nursing bouts and nursing attempts.

7. *Milk Stealing.* All nursing failures and successful nursings made by kids other than the offspring of the focal mother, and all attempts that the focal kids made to nurse from mothers other than their own.

8. *Milk Yield and Composition.* The Dairy Goat Facility performed a standard analysis of the milk of each adult female once: when their kids were 52 days old. A timed-milking (Oftedal, 1984) procedure was used to collect the milk. The milk composition data included the complete morning and afternoon milkings of one day. Two measures are reported here: quantity (yield in pounds) and fat content (in pounds).

Statistical Analyses

Twins were treated as statistically independent from each other, because their scores on most variables were not correlated. Also, previous studies with goats found that intra-litter variation in behavior is as large as inter-litter variation (Klopfer & Klopfer, 1977; Ruiz-Miranda, 1992). For the statistical analyses of sex and litter size differences of all variables, except body weight, the data for each individual were averaged across ages into first and second month. This grouping was done to maintain sample sizes because some kids were not observed at all ages because they were sick or their mothers had mastitis. The analyses of the effects of body weight, growth, and age on nursing and proximity to the mother used weekly data points. Overall tests of significance were done with Repeated Measures ANOVA using SYSTAT (Wilkinson, Hill, & Vang, 1992), and for post-hoc comparisons we used one-way ANOVA. Correlations were calculated with Pearson's Product-Moment test. Continuous variables were normalized with Log transformation and frequencies variables were normalized using a Square Root transformation. Significant p values were at $p < 0.05$.

RESULTS

Maternal Variables

The only significant correlations were between milk yield and maternal age (r = .83, $p = 0.0001$) and maternal weight (r = .87, $p = 0.0001$). The difference in Milk Yield between does with twins (Mean = 8.62, SD = 2.05) and singletons (Mean = 9.11, SD = 2.89) was not statistically significant (F (1,14) = .16, $p = 0.69$). There was no significant weight difference between does with twins and does with singletons (F (1,15) = .001, $p = 0.91$). Milk Yield was found to be moderately correlated with Time Nursing at 47 days (r = .57, $p = 0.02$), but weakly correlated to Kid Weight at 47 days (r = .36, $p = 0.17$). Therefore, although larger goats tended to produce more milk, this did not affect nursing and growth of kids in any systematic way.

Age of Kid

Kid age had a significant effect on all nursing behavior measures. Time spent nursing declined with age (F (6,15) = 7.38, $p = 0.0001$), as did the length of individual nursing bouts (F (6,15) = 2.92, $p = 0.03$). Nursing success significantly declined with age (F (6,15) = 1.83, $p = 0.04$), and the number of nursing attempts increased with age (F (6,15) = 2.71, p=0.002), The frequency of milk stealing was higher during the second month (Mean = 2.92; SD = 0.62) than during the first month (Mean = 0.82; SD = 1.33), with a peak at 33 days of age (F (1,15) = 4.76, $p = 0.04$).

The kid's age also had a significant effect on doe-kid association measures. As kids got older they initiated more of the approaches (F (6,15) =7.08, $p < 0.001$); kids initiated more than 50% of the approaches after 12 days of age. Moreover, kids spent more time in proximity to their mothers as they got older (F (6,15) = 2.34, $p = 0.04$), at least until 40 days of age.

Sex of Kids

Body weight and growth. Males tended to be heavier than females at all ages (Figure 1a, F (1,20) = 6.36, p=0.02). Weight gain was also higher for males than for females (F (1,20) = 4.02, p = 0.05).

Nursing behavior. There were no sex differences in time nursing (Table 1, F (1,20) = 0.61, p = 0.44), even though males had longer mean bout length than females (Table 1, F (1,20) = 5.02, p = 0.04), particularly during the first month of life. Males and females did not differ in nursing success (F (1,20) = .64, p = 0.43). Both the rate of nursing attempts and the nursing success (Table 2) of males and females were similar throughout the study (F (1,20) = 0.01, p = 0.92; and F (1,20) = 0.55, p = 0.47, respectively). When attempts to nurse from non-maternal does (milk stealing) were considered we found that out of 47 successful steals, 33 were made by males and 14 by females. Milk stealing was observed in 7 males and 5 females, and one of the males was responsible for 18 of the milk steals (38.3 %). Differences between the sexes in the frequency of udder presentations by the mother for both twins and singletons were not statistically significant.

Table 1. Monthly average for the proportion of time spent nursing and length of individual nursing bouts (seconds) for males and females born as singletons or twins. Month 1 = 5 to 26 days old; and Month 2= 33 to 47 days old. Numbers in parentheses are the standard deviations.

		Month 1			Month 2		
		Single	Twin	All	Single	Twin	All
Time Nursing	Male	.157 (.06)	.084 (.03)	.117 (.06)	.091 (.05)	.041 (.01)	.063 (.04)
	Female	.116 (.05)	.086 (.03)	.10 (.04)	.058 (.02)	.050 (.03)	.055 (.03)
	All	.137 (.05)	.085 (.03)	.109 (.05)	.074 (.04)	.046 (.02)	.059 (.04)
Bout Length	Male	87.49 (31.1)	63.26 (28.4)	75.38 (29.7)	48.92 (24.7)	36.46 (9.6)	42.69 (17.1)
	Female	52.34 (15.2)	47.72 (19.3)	50.03 (17.2)	35.01 (4.8)	35.71 (11.8)	35.36 (8.3)
	All	69.92 (29.6)	55.49 (24.5)	62.71 (27.0)	41.96 (18.3)	36.08 (10.3)	39.02 (14.3)

Table 2. Monthly averages for Nursing Attempts (successful + unsuccessful/ time) and Nursing Success (successful attempts/ total number of attempts) for male and female kids born as singletons or twins. Month 1 = 5 to 26 days old; and Month 2= 33 to 47 days old. Numbers in parentheses are the standard deviations.

		Month 1			Month 2		
		Single	Twin	All	Single	Twin	All
Nursing Attempts	Male	.05 (.02)	.223 (.11)	.145 (.12)	.197 (.09)	.296 (.20)	.251 (.16)
	Female	.09 (.02)	.149 (.09)	.122 (.08)	.251 (.21)	.274 (.14)	.264 (.17)
	All	.071 (.03)	.186 (.11)	.134 (.09)	.224 (.16)	.285 (.17)	.257 (.16)
Nursing Success	Male	.723 (.12)	.378 (.12)	.535 (.21)	.423 (.19)	.275 (.17)	.342 (.19)
	Female	.676 (.05)	.563 (.10)	.614 (.10)	.416 (.25)	.313 (.13)	.360 (.19)
	All	.699 (.09)	.471 (.14)	.575 (.17)	.419 (.21)	.294 (.15)	.35 (.19)

Approaches and proximity to the mother. There were no statistically significant differences between males (Mean for month 1 = 0.59, SD = 0.14; Mean for month 2 = 0.81, SD = 0.08) and females (mean for month 1 = 0.62, SD = 0.19; Mean for month 2 = 0.79, SD = 0.05) for the proportion of approaches initiated by the kids (F (1,20) = 0.02, p = 0.90). The differences between males (Mean for month 1 = 0.55, SD = 0.26; mean for month 2 = 0.44, SD = 0.21) and females (Mean for month 1 = 0.59, SD = 0.25; Mean for month 2 = 0.52, SD = 0.19) for the time in proximity to the mother were also not statistically significant (F (1,20) = 0.61, p = 0.44).

Other behavioral differences. Behavioral differences related to energy acquisition and expenditure did not explain the differences in body weight and growth between the sexes. Time spent resting was similar for males (Mean = 0.32 s, SD = 0.12) and females (Mean = 0.29 s; SD = 0.10; F (1,20) = 0.58, p = 0.45). The differences between the males (Mean = 0.10 s, SD = 0.06) and females (Mean = 0.09 s, SD = 0.03) in amount of time spent foraging were not statistically significant (F (1,20) = 0.54, p = 0.47).

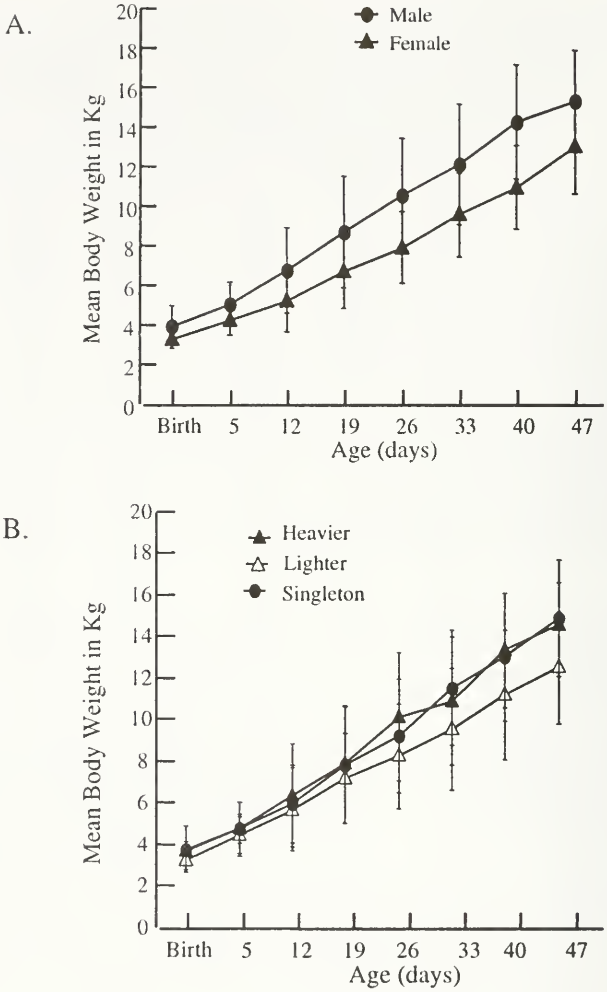

Figure 1. Body weight (mean and standard error) of A. Male and female kids from birth to 47 days of age, and B. Singleton and twin kids from birth to 47 days of age. Data from the twin kids is divided according to relative weight category.

Twins versus Singletons

Body weights and growth. The relationship between body weight and litter size was more complex than the effect of kid gender. Overall, the differences between twins and singletons in body weight (Figure 1b) and growth were not statistically significant (Weight: F (1,20) =

0.32, $p = 0.57$; Growth: F (1,20) = 1.52, $p = 0.23$). However, one of the twins tended to be heavier than the other (Figure 1b). All twin pairs showed the light-heavy relationship, and in the the mixed sex pairs the heavy twins were the males (Table 3). The average weight for heavier twins was equal or higher than that of singletons, whereas the average weight of the lighter twins was always lower than the one of singletons.

Nursing Behavior. Singletons did not differ from twins in duration of individual nursing bouts (F (1,20) = 1.84, $p = 0.19$), but nursed more frequently (F (1,20) = 4.4, $p = 0.05$), resulting in a greater time spent time nursing (see Table 1; F (1,20) = 7.41, $p = 0.01$). Nursing success (Table 2) was significantly higher for singletons than for twins (F (1,18) = 11.31, $p = 0.003$). These differences were not caused by a lack of effort from the twins; the rate of nursing attempts (Table 2) was higher for twins than for singletons throughout the study (F (1,20) = 3.72, $p = 0.06$). When attempts to nurse from does other than the mother (milk stealing) were considered we found that out of 47 successful steals, 39 were done by twins and 8 by singletons. Out of the 12 kids involved in milk steals 8 were twins and 4 were singletons, and one twin was responsible for 18 of the steals (38.3 %).

Table 3. Actual body weight (Kg) growth rate (Kg/day), proportion of times subject displaced sibling from udder (Displacer) and classification into weight categories for each kid in a twin pair. Adjacent kids in the table are siblings.

Kid ID	Mother ID	Sex of Kid	Birth Wt	Weight Month 1	Weight Month 2	Growth Rate	Weight Category	Dis-placer
0024	8054	Female	3.4	11.34	14.60	.25	Lighter	.18
0025	8054	Male	4.2	14.97	16.87	.29	Heavier	.82
0028	9046	Male	4.0	12.24	15.87	.25	Heavier	.33
0029	9046	Male	3.6	11.34	14.97	.24	Lighter	.67
0040	9034	Male	3.2	10.34	13.15	.21	Heavier	.91
0041	9034	Female	2.7	6.80	10.43	.16	Lighter	.09
0046	9065	Female	3.4	7.71	14.87	.24	Same	.45
0047	9065	Female	3.5	8.62	14.97	.24	Same	.55
0074	9070	Female	2.6	5.44	9.25	.14	Lighter	.14
0075	9070	Male	3.1	6.80	12.24	.19	Heavier	.86
0078	6035	Female	3.7	6.8	10.43	.14	Lighter	.00
0079	6035	Male	4.0	7.71	13.15	.19	Heavier	1.00

Litter size did not have a significant effect on the frequency of mothers presenting their udders to kids (F (1,20) = 2.65, $p = 0.11$). The trend was, however, for singletons (Mean for month 1 = 20.70, SD = 14.10; Mean for month 2 = 3.80, SD = 4.49) to receive more udder presentations than twins during both months (Mean for month 1 = 14.17, SD = 12.15; Mean for month 2 = 1.0, SD = 1.35). Variation among each group was high and probably accounts for the lack of significance.

Competition and displacements. With twins pairs it was possible to look at sibling competition for udder access by recording the number and pattern of displacements from the teats. We emphasized two variables, body weight and sex (Table 3). The overall main effect of sex was statistically significant (F (1,6) = 8.82, $p = 0.02$), with males displacing females more often than the opposite. Body size had a significant main effect in both mixed sex and single sex twin pairs. The Heavy kids displaced their twins more often than the reverse (F (1,10) = 17.22, $p = 0.002$). Differences between Heavy and Light twins in Time Nursing were not statistically significant (F (1,10) = .15, $p = 0.70$).

Approaches and proximity. Even though the overall effect of litter size was not statistically significant (F (1,20) = 2.73, $p = 0.11$), twins (Mean = 0.67, SD = 0.15) initiated more approaches than singletons (Mean = 0.53, SD = 0.16) during the first month (F (1,20) = 4.79, $p = 0.04$). Singletons (Mean for month 1 = 0.67, SD = 0.22; Mean for month 2 = 0.58, SD = 0.16) spent significantly more time in proximity to their mothers than twins (Mean for month 1 = 0.48, SD = 0.25; Mean for month 2 = 0.39, SD = 0.19) throughout the study (F (1,20) = 7.07, $p = 0.02$).

Resting and foraging. The difference in resting behavior between singletons (Mean = 0.32; SD = 0.59) and twins (Mean = 0.29; SD = 0.64) was not statistically significant (F (1,20) = 1.2, $p = 0.28$). The differences between singletons and twins in amount of time spent foraging were not statistically significant (F (1,20) = 2.54, $p = 0.12$).

DISCUSSION

Milk allocation was more affected by litter size than by sex of young, although there might be an interaction between both factors, kids played an active role in the allocation of milk and its conversion to body weight, and early mother-young interactions were different for twins and singletons. The relationships between age of kid and behavioral variables follow the same patterns seen in field studies of wild bovids (Byers & Moodie, 1990; Green, 1992; Hass, 1990; Schaller, 1977), and more naturalistic studies of domestic ruminants (Ewbank, 1967; Lickliter, 1984, 1987; Mandiki, Fossion, & Paquay, 1989; Peña Blanco, Herrera García, Subires Antúnez, & Aparicio Macarro, 1985; Reinhardt & Reinhardt, 1981).

Resource Allocation

We found that males were heavier than females from birth to day 47. One might expect then that males had more access to post-natal resources from the mother, but that was not true for time nursing, nursing success, and nursing attempts. Other domestic bovids show this pattern of sex differences in size but no sex differences in nursing behavior (Burfening, 1972; Plasse, 1978; Reinhardt & Reinhardt, 1981). So, how do males grow larger than females? It is possible that male kids obtained more milk per unit time. Males had a longer nursing bout length than females, and this can result in higher milk (or milk fat) per unit of time, especially if the first few seconds of suckling are "dry" compared to the last few seconds (Oftedal, 1985). However, available data shows that there are no sex differences in milk consumed in hand reared kids fed milk ad-libitum (Hadjipanayiotou, 1986) or twice per day (Peña Blanco, et al., 1985). Males could be more efficient at converting milk into body weight than females, but there are no data to test this alternative. It is also possible that males procured milk or other nutrients elsewhere or that males had different activity budgets than females. The only data germane to this hypothesis is the slight male bias in milk stealing observed. All of these alternative explanations suggest that to explain growth differences between sexes we should be looking at physiological and behavioral traits of kids, as well as at female resource allocation.

Being a twin or a singleton had a significant effect on milk allocation and interactions with the mother, but not on body weight. On average, twins did not differ from singletons in body weight, although among twin pairs there was always a smaller twin which weighed less than singletons. Although the weight differences among twins can be partially explained by the sex differences (4 of 6 pairs were of mixed sex), the differences were also present in same sex pairs (one male-male and one female-female). A study with larger sample size is necessary to corroborate our observations. Singletons were more successful in their solicitations, nursed longer, and spent more time in proximity to their mothers than twins. Also, mothers with singletons sought their kids more often than mothers with twins, and stayed closer to them. Differences in nursing behavior were surprising since dairy goats are thought to produce enough excess milk to feed several kids. However, in this study does with twins did not produce twice the amount of milk than those with singletons, and thus milk supply was more limited for twins.

The lack of a strong litter size effect on body weight is in contrast with studies carried out on 'meat' goat breeds and other domestic bovids. In meat goats, singletons obtained more milk and gain more weight than twins (Figueiredo, Simplicio, Bellaver, & Pant, 1982; Hadjipanayiotou, 1986). Meat goats are smaller and produce less milk (mean=4.26 (.33) kg/goat/day) than the dairy goats used here (5.31 (.20) kg/goat/day). Milk is in more limited supply for twin meat goats than for twin dairy goats. Singletons were heavier than twins at all ages in Clun Forest and Texel sheep, even though twins had longer suckling bouts and higher total duration of suckling than singletons during the first 5 weeks of lactation (Ewbank, 1964, 1967; Mandiki, *et al.*, 1989). In cattle with twins, the mother-young bonds are weaker resulting in calves seeking out allonursing, weaning earlier, and poorer growth than singletons (Price, *et al.*, 1984/85). These results are different from those obtained in pronghorn antelopes where there were no litter size differences in nursing behavior (Byers and Moodie, 1990). None of these studies reported intra-litter variation in body weight or milk intake for twins.

Sibling Interactions

This study presents evidence for sibling competition. One twin tended to be heavier, obtained more milk, and was the displacer more often than the other. As in previous studies with goats (Klopfer & Klopfer, 1977), evidence for maternal buffering came during the first hours post-partum; the does did not engage in nursing until both young had been born. After that mothers nursed their kids regardless to the order of arrival and without interfering after nursing had commenced, even when one kid displaced another or when both kids were fighting over teat access. Most intra-litter differences related to competition were seen during the first month of life, a time when the female should have been able to exert control over resource allocation. It seems that in goats maternal buffering occurs only early in the life of kids, later kid's aggressiveness and competition between siblings determine the nature of suckling behavior.

There is scant evidence available of intra-litter competition in domestic or wild artiodactyls. In sheep, Burfening (1972) recorded an interaction between sex and litter size, where male lambs in mixed sex pairs always grew larger than females and than males in same-sex litters. Price *et al.* (1984/85) found in a study of free-ranging cattle that one twin was more adept at milk stealing than the other, which stayed suckling the mother more. It is not known which was the heavier calf or the sex of the calves. Studies of intra-litter competition in wild ungulates and feral domesticates are necessary to characterize the nature of parent-young interactions more fully.

Control of Resources

The effect of sibling competition on nursing and mother-young interactions, and the observation that sex differences in nursing were most evident in kid behaviors, and not in maternal behavior suggest that kids were an active participant in controlling the allocation of resources. Does sometimes tried to avoid nursing and avoided the kids; the kids responded by pursuing the female and often blocked the female's path until she stood and nursing commenced. The few studies reported that describe the role of the young in the procurement of resources suggest that the allocation of resources in ungulates is not completely under the control of adult females. For example, lambs have different strategies for approaching an ewe for nursing; if it is their mother they adopt a frontal approach and if it is an alien ewe, they approach from rear or side (Poindron, 1976). Similarly, water buffalo calves are active and successful solicitors of milk from their mothers and alien cows, and use a variety of approach behaviors when dealing with either. They follow a strategy of maximizing the total number of solicitations rather than the probability of success (Murphey, Paranhos da Costa, de Souza Lima, & de Moura Duarte, 1991; Murphey, Paranhos da Costa, Gomes da Silva, & de Souza, 1995). These imply that selection processes have acted during ontogeny to produce young with flexible behavioral strategies to obtain milk. Whether individuals have different strategies or one, and the relative benefits and costs of each has not been studied in any detail.

Byers and Moodie (1990) argued that in those wild ungulates that show male bias in provisioning during lactation growth rate is slow, and females are likely to be able to produce enough milk to invest extra on males; whereas in species with high growth rates the mothers can not show provisioning biases during lactation. To this we would like to add litter size as an intervening variable. Oftedal (1985) argued that species that twin regularly have high costs of lactation, and thus male-biased nursing would likely be seen in singletons and not in twin litters. Most of the ungulates in which there are no sex differences in nursing behavior or growth during lactation are species that twin regularly (see Byers & Moodie, 1990). The lack of sex differences could be caused by a combination of limits in milk availability for twins, and the inability of mothers to control allocation of milk among their precocial young. For sexually dimorphic species, if males are not getting more milk than females, they must procure more food elsewhere either as milk theft or foraging, have more efficient digestion and conversion of food to weight, or expend less energy than females. These suggest that there is strong selection for specific traits of young males that enable them to obtain more resources. The active role of offspring is likely to be an important determinant of parental resource allocation in precocial species with multiple offspring.

The results of this study should be replicated under more naturalistic conditions than corraled dairy goats, or a captive study with more twin litters of same sex and mixed-sex, as well as triplets. Our sample may have been inadequate to detect small differences between sexes or litter size. Domestic rumiants are a good model to study these problems because breeds differ significantly in lactation curves, litter size, growth rates, temperament, and adult body size among others (Frisch & Vercoe, 1978; Gipson & Gorssman, 1990; Hohenboken, 1986; Plasse, 1978). Future studies should compare low milk yield goats with high milk yield breeds under different nutritional regimes.

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