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Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex

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Abstract. The nursing behaviour of marked bighorn ewes, *Ovis canadensis*, and their lambs was observed in Alberta, Canada, for 2 years. Suckle duration decreased as lambs grew older. Nursing behaviour in mid-lactation was correlated with maternal condition; young ewes, ewes with high faecal counts of lungworm (*Protostrongylus* spp.) larvae, and ewes whose lambs were born late allowed shorter suckles and were less likely to nuzzle their lamb's rump during a suckle. Sons did not appear to receive more milk than daughters. Suckle duration in mid-lactation was correlated with survival for female lambs but not for males. Lambs born late were disadvantaged, probably because nutritious forage was accessible to their mothers only in early lactation.

Lactation is a process of fundamental importance among mammals, for both its nutritional and social significance (Wilson 1975; Pond 1977). Individual differences in nursing behaviour should have a profound effect on the lifetime reproductive success of females. While the effects of individual variation in milk production are well known for domestic species (Doney & Munro 1962; Munro 1962; Butterworth et al. 1968), little is known about the sources of variation in individual milk production and maternal behaviour among wild ungulates. The objectives of this study were to determine whether nursing behaviour affected the survival of bighorn, *Ovis canadensis*, lambs, and to explore the effects of lungworm infection, ewe age, timing of lamb birth, lamb age and sex upon nursing behaviour.

The suckling behaviour of bighorn lambs has been described by Geist (1971), Shackleton (1973), Horejsi (1976), Berger (1979) and Shackleton & Haywood (1985). Horejsi (1976) proposed that the frequency with which a ewe nuzzled the lamb's rump during suckles was a measure of maternal care. In this study, this hypothesis was tested by determining the frequency of nuzzling for individual ewes. Suckle duration decreases through lactation; the decline is steeper during the first month and gradual from then to weaning (Horejsi 1976; Berger 1979). Shackleton & Haywood (1985) reported that for lambs younger than 2 weeks there were two types of suckles: long suckles that occurred after the ewe had been resting, and probably had a major nutritional function, and short suckles while the ewe was active, that may have reinforced the mother–offspring bond without supplying much nutrition.

Bighorn sheep are infected by nematode lungworms (Uhazy et al. 1973). Parasites tax their host's metabolism and may obtain resources that could otherwise be used for reproduction (May & Anderson 1978; Hudson 1986; Saumier et al. 1986). Previous research (Festa-Bianchet & Samson 1984) revealed that lambs of ewes with high faecal counts of lungworm larvae were less viable than lambs of ewes with low faecal counts. Therefore, I hypothesized that ewes with high faecal counts of lungworm larvae would provide less milk for their lambs and would be less attentive mothers.

Young females that reproduce before completing body growth must invest a greater proportion of their resources to provide the same level of maternal care (including milk production) as adult females (Green 1986; Stewart 1986). Bighorn ewes in Alberta can lamb at 2 years of age (Festa-Bianchet 1988), but do not reach adult weight until their fourth summer (Jorgenson & Wishart 1984). Thus, parous 2- and 3-year-old ewes bear at the same time the energetic costs of growth and lactation, and may be expected to allow their lambs to suckle for shorter times than older ewes.

Ewes require access to forage with high protein content to ensure adequate milk production (Munro 1962; Arman et al. 1974; Berger 1979). Reviews of temporal variations of lambing date in *O. canadensis* and *O. dalli* have emphasized the role of vegetation phenology: lambs should be born just before the peak in forage growth and protein content (Bunnell 1982; Thompson & Turner 1982).

Horejsi (1976) suggested that ewes that gave birth late would miss this peak and would be unable to produce sufficient milk in mid- and late lactation. Thus, it was expected that lambs born late would be allowed shorter suckles than lambs born earlier.

In a polygynous species such as bighorn sheep, where the reproductive success of males is probably dependent upon body size (Geist 1971), females may be expected to invest more in sons than in daughters (Trivers 1972; Clutton-Brock et al. 1982). A ram may have a small chance of reproducing unless it can reach a very large size, while a ewe's reproductive performance is relatively less dependent upon body size. Therefore, it was expected that sons would be allowed longer suckles than daughters.

MATERIALS AND METHODS

The study was conducted in the Sheep River drainage in southwestern Alberta, Canada. Horejsi (1976) had previously studied the suckling behaviour of bighorn lambs in this area. Sheep were captured with tranquillizing drugs and marked with plastic ear tags. No lambs were captured before 21 August. The age of newborn lambs was estimated at first sighting by their behaviour and location relative to the lambing grounds. More details on the study area, populations, methods of capturing, censusing, and aging lambs, are provided elsewhere (Festa-Bianchet & Jorgenson 1985; Festa-Bianchet 1986, 1988). Data on maternal behaviour were collected in 1984 and 1985 from 49 marked ewes that produced 76 singleton lambs over the 2 years. Observation time was 427 h in 1984 and 358 h in 1985. Observations lasted for 2–10 h per day, and were evenly distributed from 0530 to 2030 hours. Observations were conducted during 70% of the days from late May to mid-September, and during 8–10 days from mid-September to early October. Because of their wide distribution and frequent movements (Festa-Bianchet 1986), it was not possible to observe all lambs during all periods, nor for equal amounts of time. An attempt was made to sample the largest possible number of lambs by alternating observations between the two main ranges of the ewe group (Festa-Bianchet 1986).

Bighorns were observed with Zeiss 15 × 50 binoculars mounted on a tripod. Data were spoken into a tape-recorder and later transcribed. All suckle attempts by all lambs within view were recorded during observations. Suckles were classified as successful if they lasted 5 s or more, according to Horejsi (1976) and Gauthier & Barrette (1985). Only 2·6% of suckle attempts lasted 1–4 s: these were considered unsuccessful, together with cases when the ewe did not allow the lamb to suck. For successful suckles, I recorded whether or not the ewe nuzzled the lamb's rump. Suckle duration was timed to the nearest second with a stopwatch. I also noted whether the ewe or the lamb terminated the suckle.

The nursing season was divided into eight 15-day periods. Period 1 started when each lamb was estimated to be 5 days old, therefore lambs were about 124 days old at the end of period 8. The first 4 days of life were excluded because very few suckles, from only six lambs, were timed during this period.

Analyses were performed separately for data collected during early (periods 1 and 2), mid- (periods 3 and 4) and late lactation (period 6 through 8). This was done to minimize the confounding effects of lamb age, and of possible changes in the functions of suckling, from mostly nutritional in early and mid-lactation to mostly social in late lactation. In addition, some lambs were observed only in early lactation (including 10 that died at 2–6 weeks of age), while others were observed only later.

During periods 3 and 4 in 1984, an average of 10·6 suckle attempts per lamb were observed, and 5·2 suckles per lamb were timed; in 1985 these figures were 17·7 and 10·8, respectively. During periods 6–8 in 1984, an average of 8·7 attempts per lamb were recorded, and 3·8 suckles per lamb were timed; in 1985; the corresponding figures were 7·5 and 4·1. The average suckle duration for each lamb was used for analyses. Suckles lasting between 5 and 8 s (1·4% of all suckles timed) were considered successful but were not included in the calculation of average suckle duration, because most of these short suckles appeared to result from the ewe being disturbed, either by perceived predators or by other sheep.

To compare the frequency of nuzzling, seven successful suckles were selected at random from lambs for which at least that many were available in periods 3 through 5. Each lamb was then assigned a score from zero to seven representing the number of suckles when the ewe nuzzled it. A similar procedure was followed to assign a score for suckling success, except that since more data were

available, 10 suckle attempts were randomly selected for each lamb. Period 5 was included in these analyses to provide a larger sample of lambs for which the minimum number of suckles (7) or suckle attempts (10) had been recorded. The inclusion of period 5 did not affect the outcome of analyses, since no differences in nuzzling or success rate existed between periods 3 and 5 in either year (Festa-Bianchet 1987).

Faecal samples were collected from marked ewes ($\bar{X}=4{\cdot}5$ samples per ewe per year) in March and April of each year. Faecal counts of lungworm larvae peak in these 2 months (Uhazy et al. 1973). The number of larvae per g of dry faeces was counted using the Baermann technique (Samuel & Gray 1982). Counts were subjected to a square-root transformation to obtain a normal distribution. The average transformed count for each ewe each year was used for data analysis. In 1982–1983, ewes whose lambs survived to October had an average transformed larval count of 23·0, while the average for ewes whose lambs died before October was 27·0 (Festa-Bianchet & Samson 1984). These figures provided an a priori distinction between low- and high-count ewes. In 1984 and 1985, ewes whose transformed count was 23·0 or less were assigned to the low-count group, ewes whose count exceeded 27·0 were assigned to the high-count group. Ewes whose count was between 23·0 and 27·0 were excluded.

Problems may arise when data are collected repeatedly from the same individuals (Machlis et al. 1985). In this study, 27 ewes were observed in both years. In most cases, potential pseudo-replication was avoided by repeating statistical analyses for each year of the study. To reduce further the chances of interdependence of data points, pooled regression analyses were first run for ewes with data in both years. Following residual analysis (Draper & Smith 1981), I eliminated one observation for ewes whose residuals were of the same sign and at least one was greater than 1 SD from the mean of all residuals. When one datum was to be eliminated, I chose the one based on fewer observations (each datum was the average of several suckles). This conservative procedure eliminated from the pooled data set repeated observations that may have biased the results of statistical analyses, and reduced the chances of Type I error. As a result, when pooled data are reported, the sample size is less than the sum of samples in the 2 years. All significant differences remain significant when all data for both years are included.

Different suckle durations for the same lamb in mid- and late lactation approximated a normal distribution, and so did the average suckle durations for all lambs. Therefore, suckling data were analysed using parametric statistics, except when sample size was small. For multiple regression and correlation analyses, lamb birthdate was coded from zero to nine according to the 5-day interval during which the lamb was born, with the first interval starting 16 May. All lambs born on or after 26 June were included in interval 9. Based on differences in reproductive success (Festa-Bianchet 1988), ewes were assigned to three age classes: 2-year-olds, 3-years-olds, and older than 3 years. Lamb sex was coded as a dummy variable (Kerlinger & Pedhazur 1973). The SPSS package (Nie et al. 1975) was used for statistical analyses. Two-tailed tests were used unless a rationale existed for a one-tailed test.

Lamb time budgets were constructed in the summer of 1984. Lambs were observed for 5–25 min after their mother had been identified, and the time spent feeding, resting and active was noted. These data allowed me to monitor the increase in feeding on vegetation as lambs became older, and to detect any differences due to lamb sex.

RESULTS

Suckle Duration

Average suckle duration decreased with increasing lamb age. The mean coefficient of variation for suckles by the same lamb in the same period was 0·56 in period 1, declining to 0·25 in period 2 and to an average of 0·18 in periods 3–8 (range 0·13–0·21). Except for one case in 1985, the ewe terminated all suckles from period 2 onward, usually by stepping over the lamb. A few suckles were terminated by lambs in period 1: 4·5% in 1984 and 7·6% in 1985. There were no differences in suckle duration between the 2 years ($P>0{\cdot}1$ for all periods).

Lambs born to ewes with high faecal counts of lungworm larvae tended to have shorter suckles in mid- and late lactation, but not in early lactation (Fig. 1). High-count ewes averaged 5·1 years of age in 1984 ($N=16$, range 2–10) and 5·5 years in 1985 ($N=19$, range 2–11). Low-count ewes averaged 6·1 years of age in 1984 ($N=18$, range 2–10), and 6·0 years in 1985 ($N=26$, range 2–11; Mann–Whitney U-test, $P>0{\cdot}05$ in 1984; $P>0{\cdot}5$ in 1985). Lamb sex

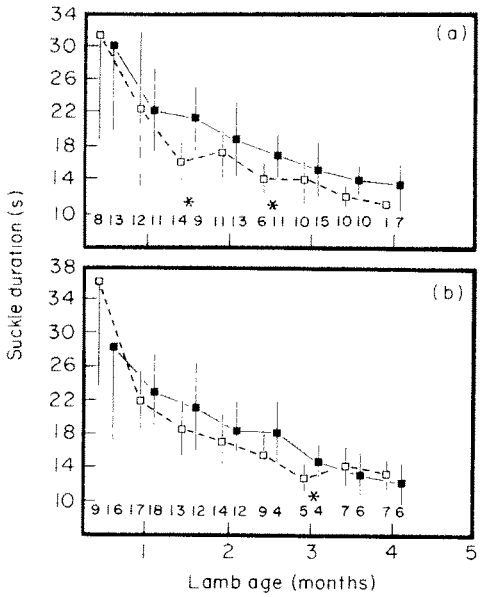

Figure 1. Duration of suckles ($\bar{X}$ and SD) of bighorn lambs born to ewes with high (□) and low (■) faecal counts of lungworm larvae, by 15-day periods in 1984 (a) and 1985 (b). Asterisks indicate significant differences (Mann–Whitney *U*-test; $P<0.05$). Numbers indicate sample size (lambs).

ratio did not differ between the two groups: in 1984 the 16 high-count ewes produced 11 males, four females and one lamb of unknown sex, while the 18 low-count ewes produced 11 males, five females and two lambs of unknown sex. In 1985, 19 high-count ewes produced eight males, six females and three lambs of unknown sex; the 26 low-count ewes produced nine lambs of each sex and seven of unknown sex.

Lambs that survived to October received longer suckles during early and mid-lactation (Table I). A one-tailed test was used here because Geist (1971), Shackleton (1973) and Horejsi (1976) suggested that suckle duration was positively related to lamb survival. There were no differences in suckle duration at age 80–124 days between lambs that died and those that survived. There were no differences in sex ratio (survivors: 25 males, 16 females; non-survivors: 16 males, eight females; $G=0.21$, NS) or in the average age of the mothers (survivors: 5·9 years; non-survivors: 5·4 years). Lamb survival in months (0–7) was correlated with suckle duration at age 35–64 days in 1985 when the ewe's lungworm larval count was controlled through partial correlation ($r=0.42$, $df=28$, $P=0.01$). This partial correlation was not significant in 1984 ($r=0.16$, $df=23$, NS), but approached significance when years were combined ($r=0.22$, $df=50$, $P=0.06$). With the pooled data, suckle duration at 35–64 days of age was correlated with survival for female ($r=0.59$, $N=22$, $P=0.002$) but not for male lambs ($r=0.03$, $N=39$, NS).

Factors affecting suckle duration for lambs aged 35–64 days (periods 3 and 4) were investigated through stepwise multiple regression. When the data were pooled, lamb sex, birthdate and ewe larval count contributed significantly to the regression model (Table II; $N=58$, $F=8.931$, $R^2=0.33$, $P=0.0001$). When data for each year were analysed separately, lamb sex and ewe larval count contributed significantly to the multiple regression in 1984 ($N=30$, $F=8.341$, $R^2=0.38$, $P=0.001$). In 1985, ewe larval count and lamb birthdate contributed significantly to the regression. The contribution of lamb sex in 1985 was almost significant ($P<0.07$), therefore it was included in the model ($N=32$, $F=5.746$, $R^2=0.38$, $P=0.003$). There were no correlations between any of the independent variables.

Ewe age was correlated with suckle duration ($r=0.29$, $N=64$, $P=0.009$), but also with lamb birthdate ($r=-0.36$, $N=72$, $P=0.001$) and did not explain any further variance when included in the multiple regression. Young ewes allowed shorter suckles in periods 3–5 (Fig. 2).

Lambs born late had shorter suckles than lambs born earlier, regardless of whether or not those born to 2-year-olds were included in the analysis (Table III). Lambs born in June had shorter suckles than lambs born in May in periods 4, 5 and 7 (Fig. 3).

Male lambs had shorter suckles than females in periods 3 and 4 (Table IV). There was no difference in maternal lungworm larval count between the sexes ($t=0.93$, NS), and median date of birth was 26 May for both sexes. Ewe larval count and lamb birthdate were better predictors of suckle duration in mid-lactation for female ($R^2=0.49$, $N=23$, $P=0.001$) than for male lambs ($R^2=0.18$, $N=39$, $P=0.026$).

Suckle durations of lambs aged 80–124 days (periods 6–8) appeared to correlate with the same variables as suckles of younger lambs, but few correlations were significant. Ewe larval count was correlated with suckle duration in 1984 ($r=-0.34$, $N=30$, $P=0.03$), and with the pooled data set the

Table I. Suckle durations of bighorn lambs that did and did not survive to weaning in 1984 and 1985

Lamb age (days)	Year	Duration (s) Lamb survived N	$\bar{X}$	SD	Lamb died N	$\bar{X}$	SD	t	P*
5–34	1984	23	27·8	10·3	7	21·4	3·0	1·59	0·07
	1985	21	26·7	5·8	21	24·6	7·2	1·04	NS
	Both	41	26·5	7·3	27	23·3	6·0	1·92	0·03
35–64	1984	24	18·1	4·0	7	16·3	3·3	1·08	NS
	1985	15	20·3	4·0	20	16·9	3·1	3·14	0·002
	Both	36	18·3	3·2	26	16·8	2·6	1·87	0·03
80–124	1984	27	13·7	2·5	3	12·5	0·5	0·81	NS
	1985	10	13·6	1·9	12	12·8	1·9	0·89	NS
	Both	34	13·6	2·4	14	12·7	1·2	1·22	NS

* One-tailed (see text).

Table II. Multiple regression analysis of bighorn lamb suckle duration (s) at 35–64 days of age in 1984 and 1985

Variables	b	SE of b	beta	t	P
(Constant)	23·13	1·24			
Lamb sex	−2·38	0·72	−0·37	−3·30	0·002
Birthdate	−0·57	0·19	−0·33	−2·96	0·005
Ewe's LPG*	−0·09	0·04	−0·26	−2·34	0·023

* LPG: transformed faecal count of lungworm larvae.

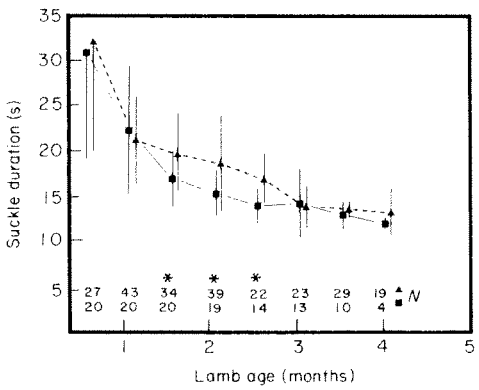

Figure 2. Duration of suckles ($\bar{X}$ and SD) of bighorn lambs born to ewes of different ages in 1984 and 1985, by 15-day periods. ▲ Ewes aged > 3 years; ■ ewes aged 2–3 years. Asterisks indicate significant differences (Mann–Whitney U-test; $P < 0·05$).

Table III. Average suckle duration (s) at 35–64 days of age for bighorn lambs born up to and after the median birthdate for all lambs in 1984 and 1985

Year	Birthdate	N	Duration	SD	t	P
1984	Early	15	19·2	4·4	2·27	0·031
	Late	16	16·3	2·6		
1985	Early	19	19·3	3·9	1·95	0·059
	Late	18	17·0	3·1		
Both	Early	32	18·6	3·2	2·66	0·010
	Late	32	16·6	2·8		
Both*	Early	32	18·6	3·2	2·43	0·018
	Late	23	16·5	3·1		

* Excluding lambs of 2-year-old ewes.

correlation approached significance ($r = -0·21$, $N = 49$, $P = 0·07$). Lamb birthdate was correlated with suckle duration with the pooled data set ($r = -0·25$, $N = 50$, $P = 0·04$). Lamb sex and ewe age were not correlated with suckle duration at 80–124 days of age. Suckle durations for the same lamb at age 34–65 days and 80–124 days were correlated ($r = -0·36$, $N = 46$, $P = 0·007$).

Suckling Success

Suckling success declined with increasing lamb age and did not differ between years (Fig. 4). The average success score during periods 3–5 was independent of sex: 6·9 for males ($N = 27$) and 6·7

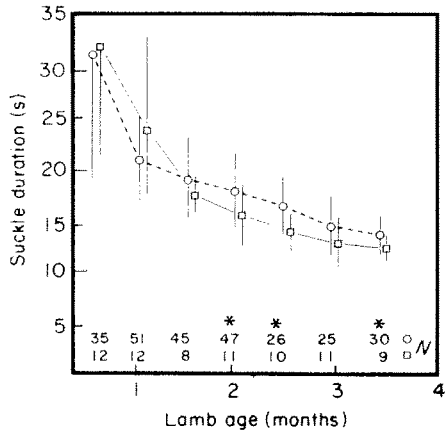

Figure 3. Duration of suckles ($\bar{X}$ and SD) of bighorn lambs born in May (○) and June (□) 1984 and 1985, by 15-day periods. Period 8 is not shown as data were not available for lambs born in June. Asterisks indicate significant differences (Mann-Whitney U-test; $P<0{\cdot}05$).

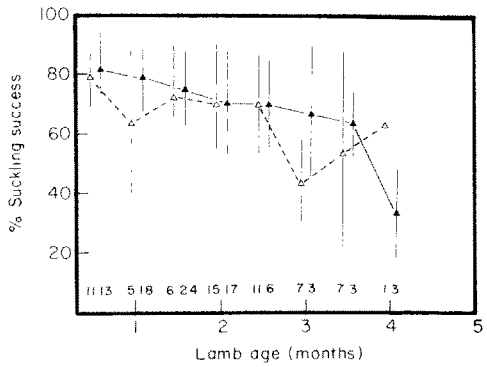

Figure 4. Suckling success (successful suckles/suckling attempts) of bighorn lambs ($\bar{X}$ and SD) by 15-day periods in 1984 (△) and 1985 (▲). Only lambs with a minimum of seven suckling attempts were included up to 2·5 months of age. Lambs with at least six attempts were included in the last three periods. Numbers just above the abscissa indicate sample size.

for females ($N=15$). Success was not correlated with ewe lungworm larval count, lamb birthdate or ewe age. Lambs that died before October had a greater success score ($\bar{X}\pm$SD$=7{\cdot}52\pm1{\cdot}47$, $N=21$) in periods 3–5 than those that survived ($\bar{X}\pm$SD$=6{\cdot}35\pm1{\cdot}61$, $N=23$; Mann-Whitney $U=571$, $P=0{\cdot}02$).

Nuzzling

The nuzzling score in periods 3–5 was positively correlated with ewe age ($r=0{\cdot}60$, $N=45$, $P<0{\cdot}001$), and negatively correlated with lamb birthdate ($r=-0{\cdot}48$, $N=45$, $P<0{\cdot}001$). Lambs born in June were nuzzled less often ($\bar{X}$ score$=3{\cdot}4$, $N=9$) than lambs born earlier ($\bar{X}=6{\cdot}0$, $N=36$; $U=79$, $P<0{\cdot}001$). Ewe age appeared to have a stronger effect than lamb birthdate upon nuzzling. The partial correlation of nuzzling score and ewe age with birthdate controlled was 0·48 ($P<0{\cdot}001$), while that of nuzzling score and birthdate controlling for ewe age was $-0{\cdot}28$ ($P=0{\cdot}03$). The nuzzling score was not correlated with larval count when all data were considered ($r=-0{\cdot}18$, $N=44$, NS), but when lambs born in June were excluded, the correlation approached significance ($r=-0{\cdot}26$, $N=36$, $P=0{\cdot}06$). If lambs born in June were excluded, males had greater nuzzling scores ($\bar{X}=6{\cdot}24$, $N=19$) than females ($\bar{X}=5{\cdot}53$, $N=15$; $U=199{\cdot}5$, $P=0{\cdot}03$).

Table IV. Average suckle duration (s) at 35–64 days of age for male and female bighorn lambs born in 1984 and 1985

Year	Lamb sex	N	Duration	SD	t	P
1984	Male	21	17·1	2·4	1·84	0·076
	Female	9	19·7	5·5		
1985	Male	19	17·1	3·3	1·91	0·066
	Female	14	19·6	4·2		
Both	Male	38	16·7	2·3	3·33	0·002
	Female	21	19·3	3·8		

Foraging Behaviour

The percentage of time lambs spent feeding on vegetation in 1984 increased with age, from 42% in late June to 70% in early September. Male lambs spent less time than female lambs feeding on vegetation in early July ($P=0{\cdot}04$) and early August ($P=0{\cdot}02$), according to Mann-Whitney U-tests.

DISCUSSION

Suckle duration is likely to be a reliable indicator of milk availability if milk is sucked by all lambs at the same rate, and suckling frequency is the same for all lambs. Both assumptions are unlikely to be completely fulfilled (Berger 1979). Nevertheless, suckle

duration appears to be a useful assessment of milk availability. In this study, suckle duration in mid-lactation was correlated with lamb survival. Previous studies have shown a correlation between average suckle duration and lamb survival (Geist 1971; Shackleton 1973; Horejsi 1976). Shackleton (1973) reported that lambs with shorter suckles suckled more frequently but still spent less time suckling than lambs with longer suckles. Suckle duration has been used to estimate relative milk consumption in red deer, *Cervus elaphus* (Clutton-Brock et al. 1982; Clutton-Brock 1984). Loudon et al. (1983) confirmed the validity of this estimate: deer calves that were allowed shorter suckles suckled more frequently, but their milk consumption was lower than that of calves allowed longer suckles.

In early lactation, the suckles of lambs that survived to October were longer than those of lambs that died before October. However, the suckle duration of lambs aged less than 35 days was not correlated with the variables considered in this study. Apparently, suckle duration in early lactation is related to lamb survival, but is not affected by the same variables that influence the duration of suckles for older lambs.

The success rate of suckle attempts is not a measure of maternal investment, because lambs that survived to October were refused suckles more often than lambs that died. Horejsi (1976) also reported a greater success rate for suckle attempts in a year of low lamb survival compared with years of high survival. Refusal rate may depend upon the frequency of attempts by the lamb, and not upon the amount of milk produced by the ewe.

Lamb Age and Weaning

The decrease in suckle duration with lamb age is similar to that reported by other studies of bighorns (Horejsi 1976; Berger 1979). Suckling success, however, did not decline as steeply with lamb age as in the populations studied by Berger (1979). The very gradual decline in suckling success confirms that weaning in Rocky Mountain bighorn sheep is slow compared with other ungulates (Geist 1971).

Weaning is a particularly difficult process to define (see Clutton-Brock & Harvey 1984). The decline in suckle duration and suckling success does not necessarily imply that older lambs receive less milk, as they may increase their intake rate and obtain the same amount of milk in less time while suckling. On the other hand, the milk received by older lambs (that had developed into functional ruminants) may have little nutritional significance, and nursing may then function mostly to reinforce the mother–offspring bond (Gauthier & Barrette 1985). Bighorn lambs in this study appeared to cease suckling at about 120–150 days of age, although suckles lasting less than 10 s were occasionally seen among older lambs.

Relationship with Faecal Counts of Lungworm Larvae

Ewes with relatively high faecal counts of *Protostrongylus* larvae allowed shorter suckles in mid- and late lactation, and appeared less likely to nuzzle their lamb's rump during suckles. Horejsi (1976) also noted short suckles and a low frequency of nuzzling at Sheep River in July 1969, a year of low lamb survival.

In February–April 1969, Uhazy et al. (1973) found very high numbers of lungworm larvae in faecal samples collected at Sheep River. High larval counts, poor maternal behaviour, and low lamb survival appear to be correlated, although larval counts did not affect suckle duration during the first month of lactation.

Ewes with high lungworm infection may have been unable to produce more milk because their energy resources were depleted by the parasites. This interpretation assumes that faecal larval count and infection intensity are closely correlated. However, faecal counts may be partly dependent upon body condition (Festa-Bianchet 1987). It seems more likely that ewes in poor condition could neither produce more milk nor limit the activities of their parasites. High larval count and low milk production may not be linked by a causal relationship, but may be two consequences of poor body condition. Possibly, the increased level of lungworm activity also increased metabolic demands for maintenance and decreased the amount of resources available for lactation (Southcott et al. 1962; Chandra & Newberne 1977).

Lamb Birthdate

Lambing of northern sheep appears to be synchronized with vegetation phenology, so that lambs are born before the peak of forage productivity (Geist 1971; Horejsi 1976; Bunnell 1980, 1982; Thompson & Turner 1982). During this study, lambs born in June and July experienced lower

survival than those born in May (Festa-Bianchet, in press).

Domestic sheep require good nutrition in late pregnancy and during lactation for milk production and lamb survival (Doney & Munro 1962; Munro 1962; Sadleir 1969). At Sheep River, forage protein increases rapidly in May, peaks in June and July and then declines (Festa-Bianchet 1987, in press). Lambs born late seemed to obtain less milk than other lambs from 1 month of age onwards. Apparently, their mothers produced sufficient milk while they still had access to high-quality forage, but later were unable to provide their lambs with nutrition sufficient for normal growth and survival. These lambs may have attempted to compensate for low milk supply by increasing their forage intake (Shackleton 1973; Robbins & Moen 1975; Horejsi 1976), but by then forage quality had declined. Thus, lambs born late may suffer in two ways from missing the peak in vegetation quality: their mothers are unable to produce sufficient milk and they do not have access to high-quality forage needed for body growth (Egan & Doyle 1982).

Ewe Age

Ewes younger than 4 years are smaller than older ewes (Jorgenson & Wishart 1984), and while lactating they also have to satisfy the energy requirements of their own body growth. Lactation is probably more expensive for young ewes because it requires investment of a relatively greater amount of resources than for older ewes. Two- and 3-year-old ewes allowed shorter suckles and were less likely to nuzzle their lambs in mid-lactation, suggesting that they were poorer mothers than older ewes. Young ewes lamb later (Festa-Bianchet 1988) and in mid-lactation face the additional problem of producing milk while feeding on forage of low protein content.

Sex Differences

Studies of feral horses (Duncan et al. 1984), red deer (Clutton-Brock et al. 1982), elephants, *Loxodonta africana* (Lee & Moss 1986) and elephant seals, *Mirounga angustirostris* (Reiter et al. 1978), provided evidence that sons received more milk than daughters. In contrast, Gauthier & Barrette (1985) did not find any differences in milk consumption for offspring of different sex in captive white-tailed deer, *Odocoileus virginianus*, and fallow deer, *Dama dama*.

In the present study, contrary to expectations, ram lambs were allowed shorter suckles than ewe lambs. However, it is unlikely that females received more milk. Ram lambs grow faster and are heavier at weaning (Jorgenson & Wishart 1984). Female lambs spent more time feeding than male lambs, while the reverse would be expected if they obtained more milk (Robbins & Moen 1975). Compensatory feeding on vegetation has been reported by Horejsi (1976) in a year of low lamb survival at Sheep River and by Shackleton (1973) in a population with short suckles and low lamb survival. Male lambs may obtain more milk per second while suckling, and empty the udder in a shorter time. They could also suckle more frequently (Lee & Moss 1986). Ewes nuzzled sons more than daughters, a possible indication of greater interest.

Survival of female lambs was correlated with suckle duration in mid-lactation, while survival of males was not. Ewes in poor condition may invest a greater proportion of their body reserves when they nurse a son. If so, the amount of milk they produce may not be as dependent upon body condition as it is when they nurse a daughter. While there are some obvious differences in the nursing behaviour of bighorn ewes with offspring of different sex, the significance of these differences remains unclear. More data on the amount of milk obtained by male and female lambs are needed. Such data are difficult to collect from wild animals, but may be obtained through a study of captive bighorns.

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