

Density-dependent mother–yearling association in bighorn sheep

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Abstract. Post-weaning mother–daughter associations are typical of many ungulates, but their existence among sheep is controversial. In bighorn sheep, *Ovis canadensis*, at high population density, strong mother–yearling associations were found involving mostly ewes whose lamb-of-the-year died at or soon after birth. At low population density, there were no mother–yearling associations regardless of maternal reproductive status. Non-lactating ewes and most ewes caring for a new lamb did not associate with their yearlings. The mother–yearling bond appeared stronger for female than for male yearlings, while maternal age had no effect. Associated yearling females had a nearly significant trend towards greater mass gain and greater body mass by the end of the summer compared with independent yearling females, but no trend was found when comparing associated and independent yearling males. Mothers that associated with their yearlings gained mass faster over the summer than mothers that nursed lambs, and by the end of the summer they were heavier than non-lactating ewes. Therefore, post-weaning association did not appear to be very costly for mothers. This study demonstrates how changes in ecological circumstances can lead to drastic changes in social organization.

The prolongation of the social bond between mother and offspring beyond weaning forms the basis of the social system of many mammalian species (Eisenberg 1966; Wilson 1975). Recently, considerable attention has been paid to post-weaning kin associations in ungulates; for example in red deer, *Cervus elaphus* (Guinness et al. 1979; Albon et al. 1992), zebu cattle, *Bos indicus* (Reinhardt & Reinhardt 1981), mountain goat, *Oreamnos americanus* (Hutchins 1984) and bison, *Bison bison* (Green et al. 1989). These studies report that mothers and daughters associate after weaning, in some cases forming distinct matriline, comparable to those observed in many primates (Gouzoules & Gouzoules 1987).

Bighorn, *Ovis canadensis*, and domestic sheep, *O. aries*, however, do not seem to fit this pattern. Festa-Bianchet (1991) found a weak association between mothers and yearling daughters in bighorns, and no association between mothers and older daughters or between mothers and yearling sons. Ewes may not benefit from associating with kin and appear attached to their home-range group (Festa-Bianchet 1986; Lawrence & Wood-Gush 1988) but not necessarily to their relatives.

Lawrence (1990, 1991) suggested that a lack of post-weaning associations was typical for wild and domestic ovids, a view challenged by reports that in some cases ewes associate with weaned daughters (Hinch et al. 1990; Rowell 1991).

Rowell (1991) and Lawrence (1991) stressed the importance of environmental factors in determining variation in ewe–offspring associations. However, little is known of how changes in the environment affect the social structure of wild ungulates. Lawrence (1991) suggested that wild sheep typically live under environmental conditions that do not favour post-weaning associations between mothers and daughters. Obviously, environmental influences on kin associations can only be discerned where such associations are variable within populations.

Among ungulates, protracted kin associations are likely to involve both benefits such as assistance in social interactions (Green et al. 1989) and costs such as increased competition (Clutton-Brock et al. 1982; Ozoga & Verme 1984). It would be particularly interesting to study the ecological circumstances that may lead to a change in the pattern of post-weaning association within a

species, as well as the life-history consequences of variation in social organization. Here, we analyse the effects of population density and maternal reproductive status on the ewe-yearling bond. Furthermore, we compare associations with yearling daughters and sons, and attempt to determine whether prolonged associations are a form of maternal investment, involving a cost to the mother, or maternal care, involving a benefit to the offspring but no measurable cost to the mother.

Increases in population density may weaken or strengthen post-weaning kin associations depending upon ecological circumstances. If food is limiting, associations may increase forage competition. Evidence that protracted association with offspring is costly to mothers has been found in red deer (Clutton-Brock et al. 1982), red-necked wallaby, *Macropus rufogriseus* (Johnson 1986) and bison (Green et al. 1989). Albon et al. (1992) reported that associations among female kin in red deer weakened as population density increased, possibly as a result of increased dispersal tendencies among females.

We were interested in a possible sex difference in mother-yearling association patterns because such a difference has been reported in many mammals (Guinness et al. 1979; Greenwood 1980; Johnson 1986) but is apparently weak in bighorn sheep (Festa-Bianchet 1991). Clutton-Brock et al. (1981) suggested that in some sexually dimorphic mammals, if mothers invest more in sons than in daughters before weaning, they may continue to care for daughters over a longer time, such that total investment in the sexes is more nearly equal.

METHODS

The Ram Mountain Bighorn Population

The study area in western Alberta, Canada (52°N, 115°W), is an isolated mountain outcrop in the Rocky Mountain foothills. The sheep use about 38 km² of alpine and subalpine habitats, from 1082 to 2173 m in elevation. Potential bighorn predators (cougar, *Felis concolor*; wolf, *Canis lupus*; black bear, *Ursus americanus*; coyote, *C. latrans*; and golden eagle, *Aquila chrysaetos*) have been observed in the area, but the extent of predation is unknown.

Sheep are captured between late May and early October in a corral trap baited with salt. Since

1976, over 90% of the population has been individually marked with ear tags or collars. For more details on the study area and capture methods, see Jorgenson et al. (1993). From 1972 to 1981, the population was kept at low density (95–110 sheep) through yearly removals of ewes. Until 1978, ewes to be removed were shot. Later, they were moved to another population. Lambs orphaned by ewe removal survived as well as non-orphan lambs (Jorgenson et al. 1993). Orphan yearling males were about 7% lighter than non-orphan males and there was no weight difference between orphan and non-orphan yearling females (Festa-Bianchet et al. 1994). The herd increased to 226 sheep in 1991 and included 195 sheep in 1992. Ewes were divided into four categories of reproductive status: (1) lactating: ewes whose lamb survived at least until October; (2) neonatal yield: ewes whose lamb died at or soon after birth; (3) summer yield: ewes whose lamb died during summer; and (4) barren: ewes that did not lactate. Lactation was determined for all marked ewes by examining the udder at capture or by observing suckles.

Sheep were observed through 10 × 50 binoculars and 15–40 × telescopes, at distances of 10–500 m. Behavioural observations, except group composition, were recorded only in 1992 and 1993. We used the Statview (Abacus Concepts 1988–1991) package for statistical analyses, and all probability values are two-tailed unless otherwise stated. We used parametric statistics to compare body weights and non-parametric statistics to compare patterns of behaviour, because we did not know whether behaviour patterns were normally distributed. The *z*-transformation of the results of non-parametric statistics is reported.

Mother-Yearling Association

From 1978 to 1984 (low density years, with an average June population of 36 ewes), and in 1990, 1992 and 1993 (high density years, with an average June population of 95 ewes), we recorded the identity of members of all groups of sheep seen each day. Groups were defined as two or more sheep that were usually within less than 50 m of each other and appeared to coordinate their activities: they stayed near each other and moved in the same direction. From these data, we derived the % association, defined as the percentage of observations when a yearling was in the same

group as its mother (Green et al. 1989; Festa-Bianchet 1991). To calculate the strength of individual associations, we used the ratio between the observed number of times the mother was in the same group as her yearling and the number expected if mother and yearling were independently distributed among groups. This association index (O/E) was used by Festa-Bianchet (1991) and it can be calculated if the total number of animals in each sex-age class in the population is known. In 1992 all association indices were either greater than 4 or lower than 2.5. Therefore, values of O/E greater than 4 (meaning that mother and yearling were seen in the same group four times as often as expected by chance) were considered indicative of association, and we used this value of the O/E ratio to group yearlings into 'associated' and 'independent' categories. To test whether mothers and yearlings were significantly associated within a certain category (for example, male yearlings, or non-lactating ewes), we tested the difference between the observed and the expected number of times each yearling-mother dyad was seen in the same group with the *z*-transformation of the Wilcoxon matched-pairs signed-ranks tests (see Festa-Bianchet 1991 for more details). Mann-Whitney *U*-tests were used to compare association indices for different groups of yearlings.

Repeated observations of mother-yearling pairs may not be independent if groups tended to be stable over many days: mother and yearling may simply remain together because they were attached to a group, not to each other. To assess the potential for non-independence of repeated observations of the same yearling, we calculated a percentage of similarity for groups containing the same yearling at re-sighting intervals of 2 and 3 days. This was the percentage of ewes in the group on the first sighting that were still in the group at the second sighting. Our calculations revealed that groups were rather fluid: from 1978 to 1984, the mean (\pm SE) percentage of similarity was 29.3 ± 4.7 after 3 days, and for 1990, 1992 and 1993, it was 21.3 ± 4.6 after only 2 days. Therefore, to limit non-independence of data points we excluded re-sightings of the same yearling at less than 3-day intervals in 1978-1984, and less than 2-day intervals in 1990, 1992 and 1993. To exclude large groups where mother and yearling were likely to occur together by chance, we used only groups including less than one-third of the total number of ewes in the population (Festa-Bianchet

1991). The average interval between re-sightings of the same yearling used in our analyses was 13.8 days in 1978-1984 and 8.9 days in 1990-1993.

Mother-Yearling Proximity

Data were collected in scan samples (Altmann 1974), at 15-min intervals. The distance in metres between mother and yearling was recorded. At the same time, we noted the identity and the distance of the mother's nearest neighbour. A chi-squared test (Sokal & Rohlf 1981) was used to test the hypothesis that the yearling was the mother's nearest neighbour more often than expected from a random distribution as described by Hinch et al. (1990). We compared the proportion of scans when independent and associated yearlings were seen closer to their mother than any other individual with a Mann-Whitney *U*-test. For these comparisons, we only used sightings when mother and yearling were in the same group.

Foraging Time and Aggressive Behaviour

We recorded data on foraging time during focal samples in 1992 (Altmann 1974). We observed yearlings for at least 40 min, until they were out of sight, or for a maximum of 2 h (\bar{X} =95 min), and scheduled sampling equally from dawn to midday and from midday to dusk. We defined foraging time as the percentage of active time (activities other than bedding) spent foraging (Owen-Smith 1979). Foraging time and percentage of activity were not affected by focal sample duration. We collected on average 1.9 focal samples per yearling for foraging time and 2.9 samples per yearling for percentage of activity. Because we averaged repeated focal samples of the same individual before statistical analysis, sample sizes correspond to the number of individuals observed. We calculated the rate of aggression received per h and compared associated and independent yearlings with a Mann-Whitney *U*-test.

Mass and Mass Gain

Body mass of all sex-age classes increased during summer. To compare body mass at the beginning and at the end of the summer, we adjusted individual body mass to the same dates. When two or more captures of a sheep were available, we calculated the individual growth rate and

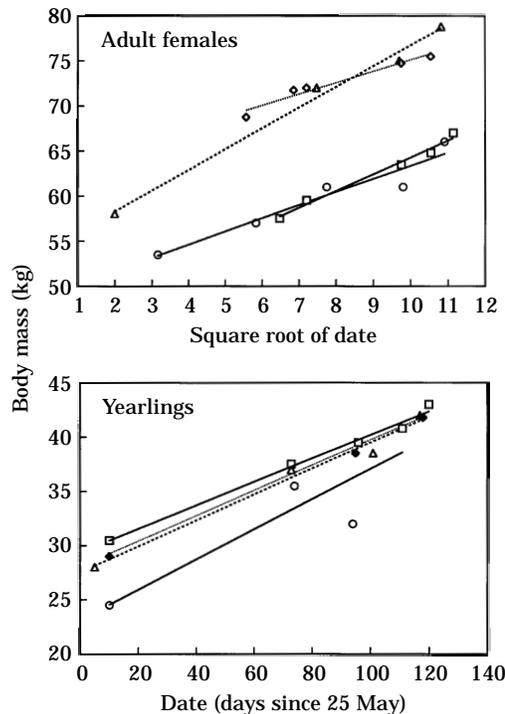


Figure 1. Increase in body mass of individual bighorn sheep during late spring and summer at Ram Mountain, Alberta, in 1992. Individuals were chosen randomly among those with the greatest number of captures.

adjusted mass to 5 June and 15 September, provided that at least 40 days passed between first and last capture. For individuals that were caught only once in a summer (less than 10% of ewes and yearlings), we calculated an overall regression for the same sex-age class and used the slope to adjust mass. We calculated adjusted mass only if a capture was available within 50 days of the date for which the adjustment was made, otherwise we excluded the individual from the sample. In most cases, the time between adjusted and measured mass was less than 10 days for 5 June and less than 20 days for 15 September. Because body mass gain of most yearlings was linear (Fig. 1), we used the regressions of mass on date. The body mass of ewes increased in a quadratic fashion, usually reaching a plateau between late July and early September. The regression of ewe mass on the square-root of date (using 25 May as day 1) was linear (Fig. 1), and we used it to adjust ewe mass. We excluded all 2-year-old ewes and 3-year-

old ewes in 1992 because none had produced a lamb the previous year, therefore none had yearling offspring. We calculated overwinter mass change by subtracting adjusted mass in mid-September from adjusted mass in early June the following year, and calculated annual mass change as the difference between mid-September mass in consecutive years.

RESULTS

Effect of Density on Association

Between 1978 and 1984, the Ram Mountain population was at low density (31–47 ewes). Out of 65 yearling-mother dyads for which at least four valid observations were available, only three had association indices greater than 4 (Table I). Overall, there was no significant association between mothers and yearlings because the number of times they were in the same group was not different from that expected if they were randomly distributed with respect to each other (Wilcoxon test: $z = -0.33$, $N = 65$, $P > 0.7$). In 1990, the population size was higher (83 ewes) but still no association was evident (Wilcoxon test: $z = -0.77$, $N = 25$, $P > 0.4$; Table I). The difference in mother-yearling association between low-density years and 1990 was not significant (Mann-Whitney U -test: $z = -0.31$, $P > 0.7$).

In 1992, yearlings and their mothers were in the same group more often than predicted by a random model (Wilcoxon test: $z = -2.71$, $N = 23$, $P = 0.007$). Out of 23 yearlings with known mothers in 1992, 10 were associated (Table I). In 1992, the mother-yearling association index for all yearlings was stronger than either in the low density years (Mann-Whitney U -test: $z = -2.65$, $P = 0.008$) or in 1990 ($z = -2.17$, $P = 0.03$). The increase in mother-yearling association followed a number of changes in population dynamics that suggested a decrease in resource availability. In 1992 there were 102 ewes, an increase of 23% from 1990. All 3-year-old ewes failed to reproduce, 43.8% of ewes were barren (compared with 17.7% in 1990) and only 23.6% were lactating (45.2% in 1990; test for the frequency of different ewe reproductive classes: $G = 13.48$, $df = 3$, $P < 0.002$). Furthermore, yearlings in 1990 gained more mass during summer than those in 1992. Females gained a mean (\pm SE) of 169 ± 9 g/day in 1990 and

Table I. Occurrence of association (associated/total and association index \pm SE) between yearlings and different categories of bighorn ewes in low-density years (1978–1984), 1990 and 1992 at Ram Mountain, Alberta

Ewe reproductive status	1978–1984		1990		1992		1993	
	Associated	Index	Associated	Index	Associated	Index	Associated	Index
Lactating	2/57	1.22 \pm 0.31	1/13	1.87 \pm 0.78	0/7	0.74 \pm 0.35	1/2	6.16 \pm 3.07
Neonatal yield	1/6	3.09 \pm 2.03	0/6	0.81 \pm 0.43	10/10	6.60 \pm 2.24	—	—
Summer yield	0/1	0.51	0/3	0.19 \pm 0.23	0/1	1.10	—	—
Barren	0/1	3.01	0/3	2.02 \pm 1.65	0/5	1.23 \pm 0.76	—	—
Total	3/65	1.42 \pm 0.28	1/25	1.43 \pm 0.33	10/23	3.41 \pm 0.63	1/2	6.16 \pm 3.07

See text for definition of association.

127 \pm 15 g/day in 1992 ($t=2.54$, $df=26$, $P=0.009$), males 169 \pm 15 g/day in 1990 and 138 \pm 9 g/day in 1992 ($t=1.71$, $df=17$, $P=0.053$).

In 1993, there were 99 ewes and only three of the five yearlings that survived still had a live mother. One yearling was not seen enough times to calculate the O/E ratio, and only one of the two other yearlings associated with its mother (Table 1).

Effect of Yearling Sex on Association

During the low-density years, there was no difference in mother-yearling associations between male ($N=26$) and female ($N=39$) yearlings (Mann-Whitney U -test: $z=-0.56$, $P>0.5$). In 1990, females ($N=18$) seemed to be with their mothers more often than males ($N=7$; $z=-2.27$, $P=0.023$). However, neither females nor males were significantly associated with their mothers (Wilcoxon test: males: $z=-1.01$, $P>0.3$; females: $z=-1.46$, $P>0.1$).

In 1992, yearlings were in the same group as their mothers in 44% of valid sightings for males and in 53% of valid sightings for females. Female yearlings were found closer to mothers than any other individual more frequently than male yearlings (Mann-Whitney U -test: $z=-2.09$, $N_1=5$, $N_2=5$, $P=0.037$). However, neither the comparison of association index values (Mann-Whitney U -test: $z=1.08$, $N_1=11$, $N_2=12$, $P>0.2$) nor that of the mean distance from the mother ($t=-1.76$, $df=8$, $P=0.058$) revealed significant differences between sexes.

Yearling Proximity to Mother

Membership in the same group does not necessarily imply a behavioural association between

associated yearlings and their mothers. Therefore, in 1992, we compared how often associated and independent yearlings were their mother's closest neighbour when yearling and mother were in the same group. Associated yearlings were the mother's nearest neighbour more often than expected by chance ($\chi^2=29.3$, $df=8$, $P=0.0003$). This was not the case for independent yearlings ($\chi^2=0.14$, $df=3$, $P>0.9$) when they were in groups that included their mother. Associated yearlings were found closer to their mothers than any other sheep more frequently than independent yearlings (Mann-Whitney U -test: $z=-2.16$, $N_1=9$, $N_2=4$, $P=0.031$).

Ewes and their associated yearlings appeared to actively maintain a bond between them. For example, when one member of the dyad was caught in the trap, the other member would often approach the trap and both would vocalize, in a manner similar to contact calls between ewes and lambs. Trapping often disrupted the composition of groups, and when released, mothers and yearlings actively sought each other. These behaviour patterns were obvious in 1992, but had not been previously observed in this population.

Effect of Ewe Age and Reproductive Status on Association

Until 1990, the few associations observed appeared evenly distributed among ewes of different reproductive status, but in 1992 all associated yearlings were with ewes that lost their neonatal lamb (Table I, Fig. 2). The association index was higher for yearlings whose mothers were neonatal yield ($N=10$) than for those with barren ($N=5$; Mann-Whitney U -test: $z=-3.06$, $P=0.002$) or lactating mothers ($N=7$; $z=-3.42$, $P=0.0006$).

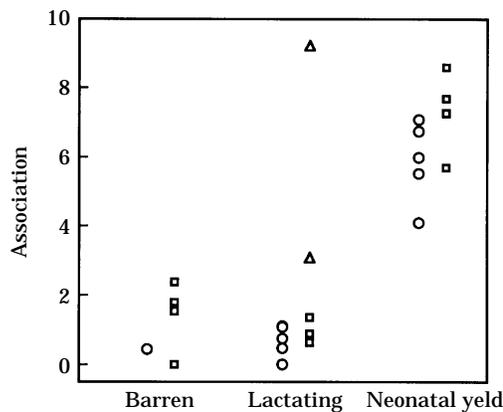


Figure 2. Association (ratio of the observations of the mother in the same group as her yearling and the number expected if mother and yearling were distributed independently among groups) for different bighorn sheep yearlings as a function of the reproductive status of their mothers in 1992 (○: males; □: females) and in 1993 (△: females).

Yearlings with barren mothers and those with lactating mothers had similar association indices in 1992 ($z = -0.81$, $P > 0.4$), but in 1993 one yearling associated with her lactating mother (Fig. 2). In 1992, no differences in age were found between neonatal yield, barren and lactating ewes with surviving yearlings (Kruskal-Wallis test: $H = 2.87$, $P > 0.2$).

Among all ewes with a living yearling in 1992, no difference was found in the age of females that associated with their yearlings ($N = 10$, $\bar{X} = 8.3$ years) and those that did not ($N = 13$, $\bar{X} = 8.2$ years; Mann-Whitney U -test: $z = -0.22$, $P > 0.8$).

Benefits of Association for Yearlings

We considered three types of possible benefit of association: foraging time, mass gain and survival. In 1992, associated yearlings neither spent more time active (Mann-Whitney U -test: $z = -1.30$, $N_1 = 9$, $N_2 = 13$, $P > 0.1$) nor received fewer acts of aggression ($z = 0.76$, $N_1 = 9$, $N_2 = 7$, $P > 0.4$) than independent yearlings. While active, associated yearlings did not spend more time foraging than independent yearlings ($z = -1.64$, $N_1 = 9$, $N_2 = 12$, $P > 0.1$). Between these two groups, no difference was found in first-winter mass change (from lamb to yearling age; Table II) for females ($t = -0.90$, $df = 5$, $P > 0.2$) or for males ($t = 0.38$, $df = 3$, $P > 0.3$).

Also no difference was found in June mass (Table II; females: $t = 0.34$, $df = 10$, $P > 0.3$; males: $t = -0.59$, $df = 7$, $P > 0.2$). Associated female yearlings tended to gain more mass during summer ($t = 1.72$, $df = 8$, one-tailed $P = 0.06$) and weigh more in September (Table II; $t = 1.50$, $df = 8$, one-tailed $P = 0.09$) than independent females but no such trend was found for males (Table II; mass gain: $t = -0.15$, $df = 6$, $P > 0.4$; September mass: $t = -0.63$, $df = 8$, $P > 0.2$). Mass gain from September 1991 to September 1992 did not differ between associated and independent yearlings (females: $t = 0.83$, $df = 4$, $P > 0.2$; males: $t = -0.24$, $df = 5$, $P > 0.4$). One-tailed tests were justified here because previous studies of ungulates suggest a benefit to offspring from post-weaning association with their mothers (Clutton-Brock et al. 1982; Green et al. 1989).

Of the 10 associated yearlings in 1992, seven attempted to suckle during observations ($N = 25$ attempts), and three yearlings were successful in eight attempts (average (\pm SE) suckling duration was 10.6 ± 1.2 s). These suckling bouts were about 40% shorter than those reported for lambs during midsummer by other studies of bighorn sheep (Geist 1971; Festa-Bianchet 1988). During focal observations, associated yearlings attempted to suckle on average every 11 h. At the end of August, udder examination of seven ewes with associated yearlings revealed that milk could be expressed from six. At that time, the udders of ewes with associated yearlings appeared smaller and more flaccid than the udders of ewes with nursing lambs. By late August, the udders of non-lactating ewes were completely regressed.

Survival to 2 years of age appeared independent of association with the mother. Because of small sample size, we combined males and females: eight of 10 associated yearlings and nine of 13 independent yearlings survived to June 1993 (Fisher's exact test: $P > 0.2$).

Cost of Association for Mothers

Our analyses did not show an effect of mother-yearling association on maternal body mass. In June, the mass of ewes varied according to reproductive status (Fig. 3; $F_{2,60} = 19.0$, $P = 0.0001$). According to Scheffé post-hoc tests, lactating ewes were heavier than barren and neonatal yield ewes. To test for differences in summer mass gain and mass in September (Fig. 3), we considered

Table II. Mean (\pm SE) overwinter mass change (from lamb to yearling age), mass on 5 June and 15 September and summer mass gain for bighorn sheep yearlings in 1992

Sex	Association	Overwinter mass change (kg)	Mass on 5 June (kg)	Summer daily mass gain (kg)	Mass on 15 September (kg)
Female	Associated	1.0 \pm 0.6 (4)	28.1 \pm 1.2 (5)	0.150 \pm 0.020 (5)	42.7 \pm 1.1 (5)
	Independent	2.1 \pm 1.3 (3)	27.5 \pm 1.5 (7)	0.104 \pm 0.017 (5)	37.4 \pm 3.4 (5)
Male	Associated	1.7 \pm 1.2 (2)	27.8 \pm 2.3 (4)	0.142 \pm 0.013 (4)	44.0 \pm 1.6 (5)
	Independent	0.0 \pm 3.4 (3)	29.3 \pm 1.4 (5)	0.145 \pm 0.010 (4)	46.0 \pm 2.8 (5)

Sample sizes are given in parentheses.

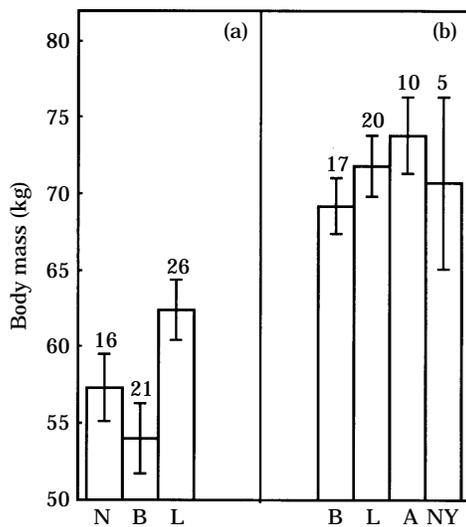


Figure 3. Mass (\pm SE) on (a) 5 June and (b) 15 September of bighorn sheep ewes of different reproductive status in 1992. N: Neonatal yield; B: barren; L: lactating; A: associated with yearling; NY: no yearling.

mothers of associated yearlings separately from other neonatal yield ewes. Summer mass gain varied between the four groups of ewes ($F_{3,53}=6.2$, $P=0.001$). Ewes with associated yearlings gained more mass ($\bar{X} \pm \text{SE} = 15.9 \pm 0.96$ kg) than lactating ewes (9.9 ± 1.25 kg); barren ewes also gained more mass (15.4 ± 1.02 kg) than lactating ewes. The regression of summer mass gain on the mother's association index for associated ewes was not significant ($r^2=0.12$, $P>0.3$). In September, the mass of ewes varied according to reproductive status (Fig. 3; $F_{3,48}=3.1$, $P=0.036$), but the only significant pair-wise difference was that associated ewes were heavier than barren ewes.

DISCUSSION

Until the study population reached very high density, our results confirmed previous findings that the typical ovid social system does not include strong post-weaning association between mothers and daughters (Lawrence 1990; Festa-Bianchet 1991). At high density, however, we found strong associations between mothers and yearlings, especially for mothers that had produced a new lamb but lost it. We suggest that the most significant characteristic of these ewes was that they had milk available (unlike barren ewes) and did not require it to care for a new lamb (unlike lactating ewes). Although suckling by yearlings was uncommon, we did see some associated yearlings suckle and attempt to suckle. The fact that we could still express milk from their mothers' udders in August strongly suggests that associated yearlings were obtaining some milk, because in the absence of suckling stimuli, milk disappears within a few weeks (personal observation). Geist (1971) and Stevens & Goodson (1993) reported suckling by yearlings in two bighorn ewe groups that they characterized as 'poor quality', with low lamb survival. Suckling by yearlings is unusual in bighorn sheep: it has not been observed in the Sheep River population (Festa-Bianchet 1991, personal observation), nor in the Ram Mountain population before 1992.

Several lines of evidence suggest that in 1992 food was becoming scarce for the Ram Mountain population. For example, ewe reproductive success and yearling mass gain were lower than in 1990 and population density had more than doubled since 1978. We suggest that the change in social organization was related to the increase in population density. Bighorn sheep may increase sociality and spatial proximity with relatives at

high population density, unlike red deer where proximity between relatives (but especially between mothers and daughters older than 1 year) declined at high density (Albon et al. 1992). Our results support Geist's (1971) and Hutchin's (1984) observations that prolonged mother-offspring bonds in some ungulates are more frequent at high population density when reproduction is more difficult.

In the migratory bighorn population studied by Festa-Bianchet (1991), yearling daughters associated more with lactating ewes than with ewes that were either barren or yeld. Festa-Bianchet (1991) suggested that the weak mother-daughter association was due more to similarity in seasonal dispersion than to a social bond: yearlings may inherit the seasonal range-use pattern of their mothers, and if their mother was not lactating, she may modify her dispersion pattern, reducing the chance of being in the same place as her daughter.

Several authors have described mother-yearling bonds as post-weaning associations (Johnson 1986; Green et al. 1989; Rowell 1991) and suckling by yearlings has been observed in many ungulates (e.g. caribou, *Rangifer tarandus*: Lent 1966; cape buffalo, *Syncerus caffer*: Sinclair 1977). Clutton-Brock et al. (1982) suggested that even if the amount of milk received by red deer yearlings was small, it could have a positive effect on growth. Hutchins (1984) reported that 64% of associated yearling mountain goats attempted suckling, but only one of 10 mothers examined was lactating. He suggested that many suckling bouts by yearlings were non-nutritive. In our study, most of the ewes that associated with their yearlings were lactating throughout the summer, and yearlings appeared to obtain at least some milk.

Our results suggest that only female yearlings may gain from the association with their mothers, because for male yearlings, there was no effect of association upon either mass gain or mass at the end of summer. If there was any advantage for males, we were unable to detect it. This result is consistent with the trend towards a stronger association with the mother for female than for male yearlings (Geist 1971; Festa-Bianchet 1991).

Protracted association with mothers may benefit yearling offspring through different mechanisms. For bison, Green et al. (1989) suggested that daughters benefited from post-weaning association through a more central position in the group (lowering predation risk) and fewer

displacements by conspecifics (improving foraging efficiency) compared with young females that did not associate with their mother. Our results, however, suggest that associated yearlings had neither a higher foraging time nor a lower rate of aggression than independent yearlings.

Alternatively, post-weaning associations may be non-nutritive expressions of maternal instinct (Ewer 1968). Mother and yearling may remain together simply because they have no behavioural mechanism that results in separation, but their continued association may not involve either benefit or cost to them. This hypothesis, however, does not explain why yearlings did not associate with barren mothers.

Mothers should wean their offspring when the cost of nursing exceeds the benefits to maternal fitness (Trivers 1974). Therefore, if post-weaning association leads to some benefits to offspring and low costs to mothers, mothers might encourage association (Green et al. 1989). Females that are not caring for a young of the year could be expected to maintain a bond with their yearling offspring (Guinness et al. 1979; Hutchins 1984; Green et al. 1989). In our population, however, yearlings associated with neonatal yeld ewes but not with barren ewes. There are two possible reasons for this difference: either barren ewes were unable to care for their yearlings because they were in very poor body condition, or yearlings did not associate with mothers that could not provide them with milk.

In early summer, neonatal yeld ewes were lighter than lactating ewes and appeared heavier than barren ewes. However, not all barren ewes were particularly small in early summer, and ewes that associated with their yearlings did not seem to bear any cost in terms of body growth. Our data suggest that prolonged associations are a form of maternal care and not of maternal investment, in contrast with the prediction that in the presence of food competition, association with weaned offspring would be costly to females (Clutton-Brock et al. 1981).

Our study sheds some light on the opposing results of different studies of ewe-offspring association in ovids. Lawrence (1991) and Rowell (1991) suggested that variability in social organization was related to factors such as the amount of available space and predation risk. We suggest that the most important environmental factors affecting mother-offspring association are

resource availability and demography. In most cases, there might not be protracted post-weaning associations of ewes and their offspring (Festa-Bianchet 1991; Lawrence 1991), because associations do not appear to benefit either mother or offspring. At high population density, however, yearlings may remain with their mothers, particularly if newborn lambs suffer some mortality.

Presence or absence of post-weaning associations in sheep appear to be plastic behavioural traits that are environment-dependent. Continued study of variation in social organization in different populations and at different population densities is needed to assess the long-term consequences of this variation for individual growth, survival and reproductive success.

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