

The social system of bighorn sheep: grouping patterns, kinship and female dominance rank

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Abstract. The social system of bighorn sheep, *Ovis canadensis*, was studied for 10 years in a marked population in southwestern Alberta. Yearling sons did not associate with their mothers. Males switched from ewe to ram groups between the ages of 2 and 4 years. No evidence of permanent emigration was found, but some rams left their native group to rut elsewhere, and the proportion so doing increased with the number of rams in the population. Most ewes coexisted with their mothers until 6 years of age, but other uterine kin, such as maternal sisters, rarely overlapped in time. Known matrilineal lines were small and 29% of the ewes had no known live adult maternal kin. The mother's survival did not affect the reproductive success of young daughters. Yearling ewes were in the same group as their mother more often than predicted by a random model, but were not in the same group as their mother for most sightings. Two- and 3-year-old ewes did not associate with their mothers. The outcome of aggressive interactions among ewes was age related, the older ewe winning 92% of interactions. When age was controlled, dominance was not correlated with reproductive success and was negatively correlated with the proportion of male offspring. The social system of bighorn sheep appears to have been shaped by anti-predator and foraging strategies that rely upon learned traditions. Kinship appears to play a limited role. There is little scope for female dominance status to affect reproductive success, because bighorns seldom require resources that can be defended against conspecifics.

In many mammals, association of female kin is thought to be the basis of the social system, for example in some sciurids (Michener 1983), primates (Gouzoules & Gouzoules 1987), ungulates (Clutton-Brock et al. 1982) and carnivores (Packer 1986). In these species, cooperation among female kin, while usually involving a cost, allows defence of a resource (space, food or offspring) against conspecifics or predators. Assistance from relatives in intraspecific interactions appears to be a benefit of kin groups in some primates (Cheney & Seyfarth 1987) and possibly some ungulates (Green et al. 1989).

To assist one another, however, relatives must coexist, and one aspect of sociality that has received little attention is the likelihood of co-occurrence of relatives. If relatives are seldom found together, one may not expect much selective pressure for cooperation (King & Murie 1985).

Relatively little is known about the ontogeny of sociality in caprins. Social behaviour among adults of different sex is mostly limited to the rut, which

has received considerable attention (Geist 1965; Hogg 1988). Wild native caprins occur in mountainous environments (Lovari 1985), are gregarious and depend upon precipitous or rocky terrain to escape predators (Geist 1971; Schaller 1977). The yearly range is typically made up of islands of habitat surrounded by unsuitable areas. Seasonal migrations are common (Festa-Bianchet 1988a), because habitat patches differ greatly in seasonal suitability through variations in snow cover, forage quality and availability of mineral licks. As a result, tradition probably plays an important role in caprin behaviour: they must know where the nearest escape terrain is situated, and must learn routes between habitat patches from conspecifics. Through protracted association with their mothers, daughters may learn the location of habitat patches, and safe routes connecting them. If intraspecific aggression was unimportant, however, traditions could be learned from unrelated individuals.

If traditions were important, one would expect them to affect dispersal of immature animals.

Males normally disperse in most mammals (Greenwood 1980). Some authors (Greenwood 1980; Dobson 1982) cite Geist (1971) as evidence that young rams disperse, but Geist does not provide data on dispersal, and little is known about dispersal in caprins.

Dominance and reproductive success appear correlated among males (Geist 1971), but Eccles & Shackleton (1986) found no correlation between dominance and reproduction, access to food, body weight changes or survival in captive females. Dominance is correlated with reproductive success and offspring sex ratio in red deer, *Cervus elaphus*: dominant hinds are more successful and produce more male offspring than subordinate hinds (Clutton-Brock et al. 1986). In bighorn sheep, *Ovis canadensis*, and in other ungulates, relatives might be selected to assist each other in dominance interactions (Green et al. 1989), if dominance and reproductive success were correlated.

Association among adult female kin has been suggested for mountain goats, *Oreamnos americanus* (Masteller & Bailey 1988), a species with dangerous horns (Geist 1965) where intra-specific aggression may be important. Among sheep, *Ovis* spp., home-range groups of ewes with traditional ranging patterns have been reported for bighorns (Geist 1971; Festa-Bianchet 1986a) and domestic breeds (Hunter & Milner 1963; Grubb & Jewell 1974). Within a home-range group of domestic sheep, all ewes have similar dispersion patterns, but relatives do not associate after weaning (Lawrence 1990).

Here I examine the roles played by kinship and female dominance status upon the social behaviour of bighorn sheep, and suggest that their anti-predator strategy has shaped social behaviour by selecting individuals that maximize security through familiarity with their home range. Both sexes rely on traditions learned from other members of their group, and kinship appears to play a limited role. Permanent emigration is rare, but rams may move to neighbouring ewe groups for the rut. Dominance is not a determinant of female reproductive success, and appears associated with female-biased offspring sex ratio.

METHODS

The Sheep River Bighorns

The study area in southwestern Alberta, Canada, includes the Sheep River Wildlife Sanctuary (50°N,

114°W), which is protected from hunting. The study population includes the Sheep River ewe home-range group (Festa-Bianchet 1986a), and the resident rams (Festa-Bianchet 1986b). The ewes winter in the Wildlife Sanctuary (1420–1740 m elevation), the rams in the Sanctuary and areas to the east. In May, ewes move to alpine ranges in the Rocky Mountains at 1800–2550 m elevation, 10–20 km west of their winter range, and return in August–October. Lambs are born in the alpine areas.

The geographical distribution of bighorn sheep in Alberta has changed little since before European settlement, and all historical ranges within 150 km of the study area are currently inhabited by bighorns. The yearly range of the Sheep River ewe home-range group overlaps the ranges of three neighbouring ewe groups, both in the Sanctuary and in alpine areas (Festa-Bianchet 1986a). Therefore, the study population had ample opportunity to experience both immigration and emigration.

The number of ewes aged 22 months or older in the study population in March increased from 49 in 1981 to 71 in 1985, then declined to 49 by 1987 following a pneumonia epizootic (Festa-Bianchet 1988b), and increased to 58 by 1990. During the study, at least six ewes were shot by hunters outside the Wildlife Sanctuary, and two were probably poached. The number of rams increased from 49 in 1982 (no estimate available for 1981) to 55 in 1985, declined to 37 in 1987, and continued to decline because of poor recruitment and hunter harvest of about one ram/year in 1986–1988, and six rams in 1989. All rams shot were 4 years of age or older. About 30 resident rams were present in March 1990.

Non-resident rams arrive in the Sanctuary in early June (spring congregation) and early October (pre-rut congregation), and join resident rams. Some resident rams move to alpine areas in summer–autumn, ranging over a wider area of mountains (approximately 470 km²) than the ewes (approximately 40 km², maps in Festa-Bianchet 1986a, b). The total range of the rams overlaps those of at least six ewe home-range groups. The rut is in late November and early December.

Capture, Marking and Data Collection

The study was based upon monitoring dispersion, survival and reproductive success of marked individuals. Data were collected between March 1981 and November 1990. Sheep ($N = 360$) were

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from hunting. The Sheep River ewe (Festa-Bianchet 1986a), and the (Festa-Bianchet 1986b). The ewes (Festa-Bianchet 1986a). There is ample opportunity for dispersal and emigration.

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2 months or older in (Festa-Bianchet 1986a). There is ample opportunity for dispersal and emigration.

in the Sanctuary (Festa-Bianchet 1986a). There is ample opportunity for dispersal and emigration.

Discussion

monitoring dispersal success of marked ewes (Festa-Bianchet 1986a). There is ample opportunity for dispersal and emigration.

captured and marked with plastic ear tags. By 1982, 85% of the ewes were marked. The proportion marked increased to over 90% by 1985, and over 95% by 1987. Adult sheep present in 1981 were aged by counting the horn annuli, a technique not very accurate for ewes older than 4 years (Geist 1966), but 93% of sheep born since 1980 ($N=274$) were caught as lambs or yearlings, and their ages were known. Most lambs were caught between August and November, so that their mothers could be identified. Fathers were not known.

I censused the Sanctuary about four times/month, except for October 1987–February 1988, October 1988–May 1989 and November 1989–April 1990. I searched the alpine range for 10–40 days each year between May and October. Details of census techniques are in Festa-Bianchet (1986a, b). I saw, on average, 97% of marked ewes during each winter census of the Sanctuary. The high (over 97%) fidelity of resident rams to the spring and pre-rut congregations (Festa-Bianchet 1986b) allowed accurate measurement of survival. Data on presence/absence of marked rams during the 1987 and 1989 ruts were provided by J. T. Hogg (J. T. Hogg, unpublished data). Frequency distributions were compared with G -tests (Sokal & Rohlf 1981).

Information on sightings of marked sheep outside the study area was solicited from field staff of provincial government agencies. Registration of shot rams is compulsory, and hunters usually provided details of tagged rams that they shot. The Alberta Fish and Wildlife Division completed winter helicopter censuses of bighorn sheep in the southern half of the province in 1983, 1988 and 1990. I participated in the 1983 survey and solicited information about ear tags from all surveys.

Calculations of Dominance and Reproductive Success

Aggressive behaviour patterns used for the calculation of dominance are described in the Results. Data on interactions among ewes were collected ad libitum between 1984 and 1989. The identity of ewes involved, and the type and outcome of the interaction were recorded. Of the 568 interactions noted, 386 had a clear outcome, with an obvious winner and loser in 301 dyads.

For the calculation of dominance, I used a modification of the index of Clutton-Brock et al. (1986), which removes the effects of age. First I calculated the ratio

$$\frac{OS_D + O_U + 1}{YS_D + Y_U + 1}$$

Where OS_D is the number of ewes of the same age or older dominated by the subject, O_U is the number of older ewes with whom the subject interacted with no clear outcome, YS_D is the number of ewes of the same age or younger that dominated the subject, Y_U is the number of younger ewes with whom the subject interacted with no clear outcome.

Unclear interactions were included because the older ewe won 92% of interactions (excluding draws) between ewes of different ages, therefore it was reasonable to assume that normally the older ewe should have won (see Results). The ratio was used to rank ewes in each cohort, then the ranks were divided by the number of ewes in the cohort, providing dominance values between 0.11 and 1.00. Ewes 3 years of age and older in 1981 were assigned to either a cohort of ewes born between 1976 and 1978 ($N=8$), or one of ewes born before 1975 ($N=5$). Cohorts born between 1979 and 1983 were each ranked separately. Dominance was calculated for 37 ewes that were seen to interact with two or more other ewes, excluding interactions whose outcome was that predictable by the age difference between ewes. Because ewes interacted infrequently, a single measure of dominance was calculated for each ewe, pooling data from interactions observed over several years. Clutton-Brock et al. (1986) employed the same procedure for red deer hinds.

Seasonal reproductive success was measured by the survival of a ewe's lamb to 1 year. The average seasonal reproductive success (number of lambs surviving to 1 year divided by the number of years of data) of the 37 ewes with known dominance index was used for comparisons with the dominance index. Seasonal reproductive success was known with certainty for non-parous ewes, or ewes whose lambs died or were marked before weaning ($N=177$ ewe-years). In 20 (10%) ewe-years, unmarked lambs survived beyond weaning. In these cases lamb survival was then assumed in each case to be equal to that year's average survival of marked lambs from the last time the unmarked lamb was identified, i.e. when it suckled from or laid in body contact with its mother (usually December to February), to the following May. Lifetime reproductive success was the total estimated number of lambs produced by a ewe that survived to 1 year of

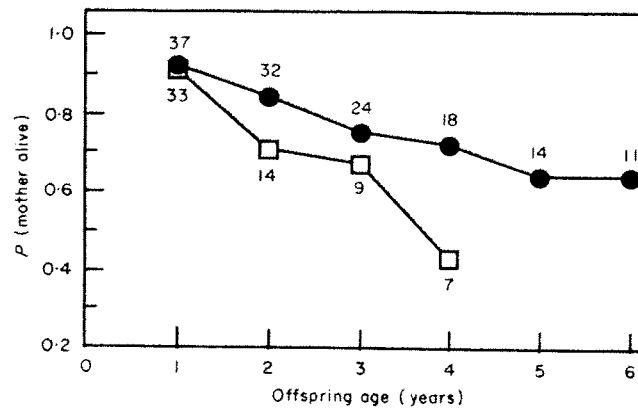


Figure 1. Proportion of bighorn sheep males (□) and females (●) whose mothers were alive by November, according to offspring age, 1982–1990. Numbers indicate sample sizes, the sample size for males older than 4 years was too small to be included. Sheep whose mother's death was artificial (shot, poached or collected) are not included.

age. Complete life histories were known for 9 of the 37 ewes above, mostly individuals that died young ($\bar{X} = 5$ years). An average of 6.2 years of reproductive data beyond 2 years of age were available for the other 28 ewes. The relationships between dominance, reproductive success and offspring sex ratio were tested with Spearman's rank correlation (r_s) with two-tailed P -values.

Association among Kin

Group size and composition (sex-age class and identity of marked sheep) were noted during censuses of the winter range and searches of the summer range. The probability that a ewe would be in the same group as her daughter (except yearling daughters) if they were distributed at random (T) was calculated as

$$T = (n-1)/(N-1)$$

Where N is the number of ewes 2 years of age and older in the population, and n the number in the group. The probability that a ewe would occur by chance in the same group as her yearling son or daughter was

$$T = n/N$$

The expected number of times that a mother and her daughter would have been seen together (E) if they behaved independently of each other was

$$E = \sum_{i=1}^t (n_i - 1)/(N - 1)$$

Where t is the number of valid sightings of the offspring from 1 May to the following 30 April.

For yearlings, n_i and N were used instead of $n_i - 1$ and $N - 1$. Valid sightings were those when (1) the group did not include more than a third of N , and (2) at least 10 days had elapsed from the last sighting used. Rule (1) excluded large groups where mother and offspring would be likely to occur together by chance. Rule (2) minimized non-independence of observations. Because of (1), the time between sightings was usually greater than 10 days: on average 8.4 valid sightings were obtained per pair per year.

The number of valid sightings when mother and offspring occurred together was compared to the expected number E with Wilcoxon matched-pairs signed-ranks tests with two-tailed P -values. To compare the frequency with which different sex-age classes associated with their mothers, the ratio of observed to expected sightings in the same group was calculated for each individual. Median ratios for different groups were then compared with Mann-Whitney U -tests or Kruskal-Wallis ANOVAs.

RESULTS

Temporal Overlap of Kin

Most yearlings of both sexes had surviving mothers, and at 5 and 6 years of age 64% of ewes had surviving mothers (Fig. 1). Males seemed to have a lower chance than females of having a surviving mother, but the sample size was small because of high mortality of young males (Festa-Bianchet 1989a). For 2-year-olds, the difference by sex was not significant ($G = 1.11$, $df = 1$, $P > 0.1$).

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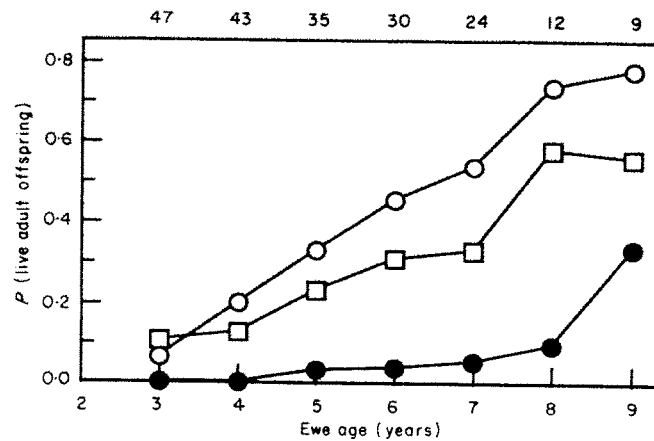


Figure 2. Proportion of bighorn ewes aged 3-8 years with surviving offspring aged 18 months or older by November, 1982-1990. □: one or more male offspring; ○: one or more female offspring; ●: two or more female offspring. Numbers above indicate sample sizes.

The proportion of ewes coexisting with adult offspring is a minimum estimate, because 18% of lambs surviving to weaning were not marked in time to identify their mothers. By 7 years of age, 54% of ewes had a surviving adult or yearling daughter; most 8-year-olds (74%) had a surviving adult of yearling daughter, and 9% had more than one (maximum of three, Fig. 2). The proportion of ewes with surviving adult daughters presumably continued to increase with age. Not many ewes, however, were much older than 8 years: for example, in 1990 only 10 ewes (17% of the ewe population) were 10 years of age or older.

Kin relationships were not known for ewes alive at the beginning of the study, and 37% of females surviving to 1990 and born after 1981 were not marked in time to identify their mothers. These problems would bias downward estimates of matriline size. The available data suggest that in November 1990 the 58 ewes in the population belonged to a maximum of 34 matriline (related as mother, daughter, sister, grandmother or granddaughter). The average minimum matriline size was 1.7, ranging from one (50% of matriline and 29% of ewes) to four.

Most of the bias in this calculation was probably due to three ewes 2-6 years of age whose mothers had not been identified but were probably still alive. When they were excluded, average matriline size was 1.8 and 25% of ewes were in matriline of one. Excluding lambs, there were only three known pairs of maternal half-sisters, and three

Table I. Number of lambs surviving to 1 year of age for bighorn ewes that survived to 4 or 5 years of age, according to whether or not the ewe's mother survived to when the ewe was 4 years old

Ewe age	Mother survived	N	No. lambs surviving		
			\bar{X}	SE	P^*
4	Yes	10	0.4	0.2	0.2
	No	7	0.7	0.3	
5	Yes	7	0.9	0.3	0.7
	No	6	1.2	0.4	

*Mann-Whitney *U*-tests.

pairs of grandmother-granddaughter. Among ewes followed from birth, one of 24 had a live adult granddaughter by 7 years of age, as did one of 12 8-year-olds and one of nine 9-year-olds.

If related bighorn ewes helped each other, one may expect greater reproductive success among ewes with coexisting kin. In particular, young adult ewes may benefit from their mother's presence. The mother's presence, however, had no effect on reproductive success (Table I).

Behaviour of Males

Yearling males were found in the same group as their mothers about as expected if they behaved independently (Table II). Analysing the data according to whether the mother's subsequent

Table II. Association between mothers and adult offspring in bighorn sheep

Sex	Age	Offspring			P*	% Together
		N	\bar{X} O/E ratio			
Male	1	19	1.29	0.28	21.2	
Female	1	32	1.53	0.04	24.8	
	2	23	1.31	0.38	24.8	
	3	16	1.35	0.47	25.1	

Only groups including one third or less of the ewes in the home-range group are considered. O/E is the ratio between the observed number of times the mother was in the same group as her offspring and the number expected if they were independently distributed among groups. % Together is the proportion of groups with the offspring that included the mother.

*Difference between observed and expected time together, Wilcoxon matched-pairs signed-ranks test.

offspring did or did not survive to weaning failed to show any difference in mother-yearling son association. Young rams remained with groups of ewes until 2 years of age, then many switched to ram groups during the spring congregation. A few yearling rams joined ram groups at this time (Fig. 3). After the spring congregation, all yearlings and about 60% of 2-year-old rams left the ram bands and most returned to female groups. Some (peak of 29% for 2-year-olds in June) formed peer groups in summer. Most 3-year-old rams joined ram groups at the spring congregation, but about 20% remained with ewe groups until 4 years of age. Again, the switch from female to male groups was associated with the spring congregation, while there was no noticeable switch during the pre-rut congregation in October (Fig. 3). The months of November to January were excluded to avoid the confusing effects of the rut, when males and females are found together regardless of age.

Emigration was not recorded during this study, but there was some anecdotal evidence of immigration. In 1988 a 3-year-old male (no. 170) was caught and tagged: this male remained with the resident ram group until the time of writing (when he was 5 years of age). This ram had a very small first horn annulus, and the only surviving unmarked male lamb born in 1985 had very large horns. Therefore, male 170 was probably not born within the Sheep River home-range group. In 1989, it appeared that three to five unmarked adult rams

(3–5 years old) joined the resident ram group, but because they were unmarked they could not be closely monitored. All 38 resident rams for which information on maternity was available were born within the Sheep River ewe home-range group, but only three male lambs from other home-range groups were ever marked. No resident ram that disappeared was subsequently reported sighted or shot in other areas. One non-resident ram caught as a lamb in 1982 was next seen in the Wildlife Sanctuary during the spring congregation 2 years later, then never seen again until it was shot by a hunter in 1988 as a 6-year-old, about 30 km from the Wildlife Sanctuary.

Because of the strong seasonality of reproduction in this population, rams could avoid breeding within their natal herd simply by leaving to rut elsewhere. Some resident rams moved out of the Wildlife Sanctuary during the rut, but 98.2% of ewes from the Sheep River group rutted in the Sanctuary ($N=326$ ewe-years). Rams of all ages left for the rut (Table III), with no age difference in the proportion that did so ($G=3.58$, $df=2$, $P>0.1$). More rams moved out for the rut in 1981–1985 (33.8%) than in 1986–1989 (18.6%, $G=4.82$, $df=1$, $P<0.04$), corresponding to a decline in the average number of resident rams 3 years of age and older at the beginning of the rut from about 40 to about 27. Most rams (81% of 116 ram-years for 43 rams) had the same rut location (in or out of the Sanctuary) in successive years, and fidelity to rut area did not vary between age-classes (Table III; $G=0.76$, $df=2$, $P>0.5$).

Behaviour of Females

Kin and group associations

Yearling ewes showed a weak tendency to associate with their mothers, and were found in the same group as their mothers 1.5 times as often as predicted by the random model (Table II). Nevertheless, they were not with their mothers in 75% of valid sightings. There was no difference between the association of mothers with yearling daughters and sons (Table II; $P>0.5$, Mann-Whitney U). Two- and 3-year-old ewes did not associate with their mothers more than expected, and there were no differences in association with the mother among ewes 1–3 years of age (Table II; Kruskal-Wallis ANOVA, $\chi^2=0.45$, $df=2$, $P>0.5$).

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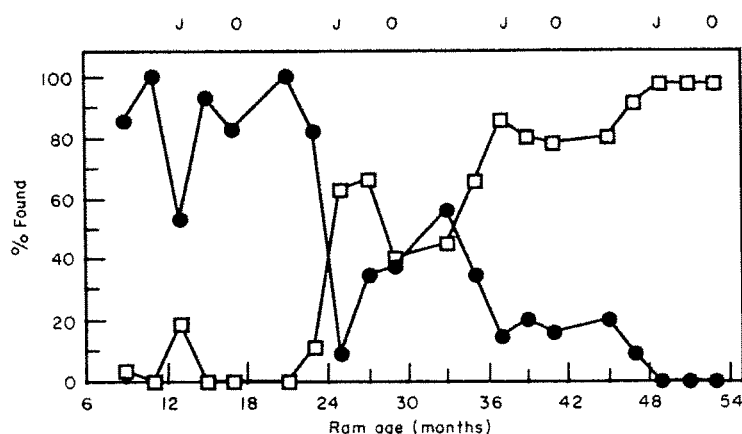


Figure 3. Proportion of bighorn rams aged 9–53 months that were found in female (●) or in male (□) groups, 1981–1989. Totals may not add up to 100% because rams found alone or in groups of yearlings and 2-year-olds are not included. Multi-year averages are shown for February, April, June, August and October each year. Sample size averaged 30 rams (range 18–35). The months of June (J) and October (O) are indicated above.

Table III. Marked resident bighorn rams that did and did not rut in the Sheep River Wildlife Sanctuary in 1981–1987 and 1989

Ram age (years)	Rut at Sheep River*		Fidelity† (%)
	Yes	No	
2–3	58 (78.4)	16 (21.6)	78
4–5	46 (67.6)	22 (32.4)	77
> 5	32 (64.0)	18 (36.0)	88
Total	136 (70.8)	56 (29.2)	81

*Numbers refer to ram-years (one ram observed for 1 year = 1 ram-year), with percentages in parentheses.

†Fidelity is the proportion of surviving rams that were in the same rutting area (in or out of the Sanctuary) in successive years between 1981 and 1987.

females are more likely to be with their mothers if the mother does not have a new calf or kid. Yearling ewes whose mothers were accompanied by a lamb, however, were found with their mothers more often (average observed/expected ratio of valid sightings: 1.77, $N=24$) than yearling ewes whose mothers either did not produce a lamb the following year, or lost it before October (average observed/expected ratio: 0.81, $N=8$, $P=0.03$, U -test).

Despite frequent contacts with neighbouring home-range groups, no ewe was known to emigrate. With one exception, Sheep River ewes spent every winter in the Wildlife Sanctuary. In 1985, a 2-year-old left in early January and was next sighted in the

alpine range in May, but since then remained with the Sheep River group and spent the following five winters in the Sanctuary.

In May, adult ewes migrate to the alpine range before yearling ewes (Festa-Bianchet 1988a), at a time when ewes from a neighbouring group are often in the Sanctuary (Festa-Bianchet 1986a). Yearling ewes from the Sheep River group mix with ewes from the neighbouring group, and presumably could emigrate into it, but were not known to do so. There was no known case of female immigration during this study.

Dominance and reproductive success

Interactions ($N=568$) between ewes included displacements (44% of interactions recorded), where one ewe walked or ran towards another and displaced her without contact, horn threats (7%), horn butts, usually directed at the rump and followed by displacement (15%), and horn clashes (34%). Most (88%) clashes had no obvious winner and loser. None of the interactions seen caused any visible injury, and ewes did not attempt to gore each other. It is unlikely that these proportions reflect the true occurrence of different types of interactions, because some (such as clashes) were more easily noticed than others (such as horn threats).

Age was a strong determinant of the outcome of aggressive interactions. For 301 dyads where a winner and loser were identified, the winner was older in 80%, the same age in 13% and younger in

ident ram group, but they could not be identified rams for which data available were born to some-range group, but in other home-range to resident ram that they reported sighted or a resident ram caught was seen in the Wildlife congregation 2 years until it was shot by a predator, about 30 km from

quality of reproduction would avoid breeding early by leaving to rut as soon as they are moved out of the rut, but 98.2% of the group rutted in the same year. Rams of all ages with no age difference so ($G=3.58$, $df=2$, $P=0.17$) did not rut in 1981–1989 (18.6%, $G=4.82$, $df=2$, $P=0.09$). There was a decline in the number of rams aged 3 years and older from about 40 to 116 ram-years for 43 years (in or out of the Sanctuary), and fidelity to rut was lower in older age-classes (Table III;

there was a weak tendency to find ewes found in the same area 1.5 times as often as expected (Table II). Never-rutting mothers in 75% of cases were found between the yearling daughters and their mothers (Mann-Whitney U -test). Two-year-old ewes associate with their mothers and there were no significant differences in the number of ewes found with the mother among different age-classes (Table II; Kruskal–Wallis U -test, $P=0.5$). (Green et al. 1989), (Festa-Bianchet 1984), yearling

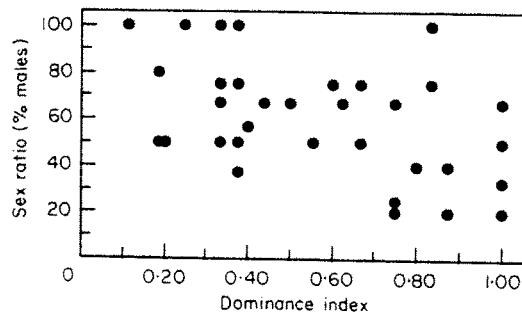


Figure 4. Relationship between dominance and offspring sex ratio for bighorn ewes.

7% (by 1 year in 11 of 22 dyads). For interactions without a clear outcome, ewes were within 1 year of age in 50% of dyads.

For cohorts born between 1979 and 1983 ($N=24$ ewes) dominance was not correlated with known lifetime reproductive success ($r_s=0.04$) or average seasonal reproductive success ($r_s=0.00$). Dominance was negatively correlated with offspring sex ratio (percentage sons, $r_s=-0.46$, $N=23$, $P<0.05$, one ewe produced no lambs). When ewes born before 1979 were included, the correlation with offspring sex ratio remained significant ($r_s=-0.42$, $N=36$, $P<0.025$; Fig. 4) and there was still no correlation between dominance and reproductive success ($r_s=0.05$). On average, the sex of 4.1 lambs was known for ewes included in this analysis (range 2–9). If dominance was computed exactly as in Clutton-Brock et al. (1986) (excluding interactions with unclear outcome), the correlations between dominance and reproductive success (lifetime and seasonal) remained non-significant ($P>0.4$) and that with lamb sex ratio also became non-significant ($r_s=0.16$, $P>0.2$).

Gomendio et al. (1990) reported that in red deer and macaques, *Macaca mulatta*, subordinate females produce more offspring of the less costly sex (female deer, male macaques). For bighorn ewes, there were no differences in reproductive success the year following production of a son or a daughter according to maternal dominance rank: reproductive success following a son averaged 0.37 for dominant ewes (dominance greater than 0.5, $N=17$) and 0.38 for subordinates ($N=15$). The year following a daughter, reproductive success averaged 0.24 for dominant ewes ($N=15$) and 0.45 for subordinates ($N=12$). Neither difference was significant (Mann-Whitney U -tests) and the trend was opposite to the prediction: subordinate ewes

had greater success after producing daughters, but their offspring sex ratio was biased towards sons (Fig. 4).

Ewes did not produce more offspring of the sex that they were better at rearing. Dominant ewes on average reared to 1 year of age 50% of their sons ($N=18$ ewes, 30 sons) and 51% of their daughters ($N=17$ ewes, 31 daughters). Subordinate ewes reared 59% of their sons ($N=16$ ewes, 38 sons) and 60% of their daughters ($N=12$ ewes, 23 daughters).

DISCUSSION

Lack of Kin Grouping

Known matrilineal groups were small, but most ewes could have formed a kin group with their mother or daughter. Most of the time, however, females were not with their mothers, as found in domestic sheep (Lawrence 1990). Apparently, kinship plays a limited role in the social organization of wild sheep, and stable home-range groups are formed mostly by non-relatives. Many ewes may be related through their fathers, but no data are available on the individual reproductive success of males, and the potential for relatedness through fathers is unknown. It is likely that ewes from the same home-range group are, on average, more related to each other than to ewes from other groups, but there is no evidence that this genetic relationship leads to any adaptive group-specific behaviour. Ewes from neighbouring groups mix freely and tolerate each other (Festa-Bianchet 1986a).

The significant association of mothers and yearling daughters may have been a result of yearlings imitating the seasonal dispersion pattern they had learned from their mothers the previous year. Individual ewes have similar seasonal ranging patterns in successive years (Festa-Bianchet 1988a), and if yearling ewes behave similarly to how their mothers behaved the previous year, mothers and daughters would often be found in the same group even if there was no social bond between them. The greater tendency of yearling ewes to be with their mothers when the latter had new lambs than when they did not is contrary to the findings in ungulates for which a protracted mother-daughter bond has been suggested (Hutchins 1984; Green et al. 1989). This behaviour may be the result of the mother changing her pattern of seasonal range use according to her reproductive status. If that is the case, a yearling ewe that adopted a seasonal dispersion pattern similar to that of her mother the previous

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For kin grouping and kin-differential behaviour to evolve, there must be some selective advantage to it. There seems to be little opportunity for bighorn ewes to cooperate with kin in food defence. Wild sheep are not known to defend food resources, with the possible exception of snow craters (Petocz 1973). I noted displacements at snow craters, but bighorn sheep mostly winter in areas with little snow cover and, unlike caribou, *Rangifer tarandus* (Barrette & Vandal 1986), it seems unlikely that access to forage in snow craters is very important. It is not obvious that two or more sheep sharing in the defence of a snow crater would forage more efficiently than if each dug its own crater, although presumably a kin coalition could displace single ewes from craters and avoid the energy cost of digging. It would be interesting to study cratering behaviour in areas where deep snow cover is common, but because bighorns usually select winter ranges with little snow cover, competition at snow craters may not have played a relevant role in the evolution of bighorn ewe social behaviour.

Bighorn ewes sometimes defend their young against coyotes, *Canis latrans* (Berger 1978a). At Sheep River, coyotes preyed upon lambs and, in at least four cases, I saw ewes chasing coyotes that approached groups of ewes and lambs. Female kin could cooperate in defending their lambs, but no cooperative defence was seen, and usually females and lambs responded to coyote attacks by fleeing to escape terrain. In at least one case, a ewe without a lamb repeatedly chased a coyote.

In some primates, related females help each other in intraspecific aggressive interactions (Silk 1983), but this behaviour was not noted among bighorn ewes. My data do not suggest that the mother's presence improves a ewe's reproductive success. A correlation between presence of kin and reproductive success would be insufficient evidence for causation, because females that are reproductively successful for any reason would have more surviving kin than unsuccessful females. Dominance had no apparent effect on reproductive success; therefore, there seems to be little opportunity for coalitions among related females to help each other increase their reproductive performance.

Bighorn sheep are very gregarious: when in small groups they are more alert and less efficient at foraging than in larger groups (Berger 1978b) and

solitary individuals are rare. A gregarious nature appears to be an adaptation to maximize security, through group alertness and selfish herd effects (Hamilton 1971). Ewes may accept the cost of being gregarious, such as increased competition for forage or parasite transmission, to decrease predation risk. They may not gain a special advantage by grouping with relatives and may be just as likely to join unrelated ewes. Ewes that only joined their relatives would be unable to form groups above the threshold (about five sheep) where alertness declines and feeding rate increases (Berger 1978b) and would probably face higher predation risk and lower foraging efficiency. Lawrence (1990) suggested that gregariousness with home-range group members in domestic sheep is more important than the mother-daughter bond.

Bighorns probably evolved under predation pressure from wolves, *Canis lupus*. These predators were rare in my study area, but their local near-extinction was only a few decades old. Cougars, *Felis concolor*, were present but seldom preyed on bighorns: only five cases were known despite the fact that most cougars in the study area have been radiocollared and monitored since 1982 (M. Jalkotzy, personal communication). The presence of wolves may increase the adaptiveness of gregarious behaviour, but I speculated that in the absence of wolves extreme gregariousness may at times be suboptimal (Festa-Bianchet 1988a).

Behaviour of Males

The move from ewe to ram groups took place gradually, over 2 years. Many young rams switched to ram groups in June, the time of the spring congregation of resident and non-resident rams in the Wildlife Sanctuary. At this time, all resident rams are in the Sanctuary, where they are joined by non-resident rams that winter elsewhere, and may form groups of over 40 rams (Festa-Bianchet 1986b). There was no indication that a similar switch occurred during the pre-rut congregation. Possibly, 2- and 3-year-old rams switch to ram groups partly to improve foraging efficiency. Yearling rams are about the size of adult ewes, but 2- and 3-year-olds are larger (Jorgenson & Wishart 1984) and probably have different foraging requirements (Robbins 1983). Differences in foraging strategy may be more important in spring and early summer than at other times, because spatial differences in forage characteristics are greatest in May-July (Festa-Bianchet 1988a).

Perhaps the most surprising aspect of male behaviour was the apparent rarity of permanent dispersal. Hoefs & Cowan (1979) also found that in Dall sheep, *O. dalli*, dispersal was rare or absent. Dispersal may be associated with inbreeding avoidance (Dobson 1982; Pusey 1987). It could be argued that some rams achieved that end by rutting within ewe home-range groups other than their native one. Avoidance of inbreeding presumably was a consequence of this behaviour, but not necessarily its adaptive reason. Young rams, with little opportunity to breed (Geist 1971; but see Hogg 1988), were as likely to move out of the Sanctuary for the rut as older rams. More rams moved out in the early years of the study, when the ram population was higher, than in the later years. The number of rams in the population may reflect the potential for intrasexual competition, and as such affect each ram's choice of rutting area: when their numbers are high, more rams may avoid competition by rutting elsewhere.

Dominance Relationships among Females

The outcome of aggressive interactions among females was strongly age-related. As in red deer hinds, individual relationships could be established when the younger ewe is 1 or 2 years old, and of considerably smaller body size than the older ewe (Thouless & Guinness 1986). Unlike red deer, however, there was no relationship between dominance and reproductive success, suggesting that in female bighorns dominance is neither important for access to resources that affect reproduction nor correlated with another character (such as body size), which may in turn affect reproductive success. Data for female ungulates indicate a variety of possible relationships between dominance, phenotype and reproductive success. Eccles & Shackleton (1986) found no consistent correlations between dominance and body mass or horn size in captive bighorn ewes. In bison cows, dominance is correlated with age but not with body mass (Rutberg 1986), but in female Apennine chamois, *Rupicapra pyrenaica*, dominance is correlated with both age and body size (Locati & Lovari, in press). In female caribou dominance is correlated with mass (Hirotsani 1990) but unrelated to antler size (Barrette & Vandal 1986).

Geist (1971) suggested that bighorn ewes may rely on few resources whose access is dependent upon intraspecific aggression, and that they may be

selected to avoid interactions in order to maximize foraging efficiency. My study supports his suggestion: dominance appears to play a limited role among bighorn ewes, and observed aggressive interactions never escalated to the point of injury.

In the Rhum population of red deer, dominant hinds have greater reproductive success and the percentage of sons produced correlates with a hind's dominance ($r_p = 0.44$, Clutton-Brock et al. 1986). The reproductive success of sons (but not of daughters) is correlated with the mother's dominance, and the reproductive cost of sons is greater for subordinate than for dominant hinds (Gomendio et al. 1990). Clutton-Brock et al. (1986) suggested that dominant hinds are likely to be high-quality individuals. Given the determinants of male reproductive success of red deer, high-quality hinds may increase their fitness by producing sons that may have very high reproductive success because of the high level of maternal investment received (Clutton-Brock et al. 1982). The red deer study, therefore, supports the Trivers & Willard (1973) hypothesis for the evolution of biased offspring sex ratios.

The determinants of male reproductive success in red deer stags and bighorn rams are similar: body size and fighting ability (Geist 1971; Clutton-Brock et al. 1982). It is likely that in bighorns, as in red deer, the importance of body size for reproductive success is greater for males than for females. Therefore, one may expect a similar dominance-related bias in offspring sex ratio in the two species. The lack of relationship between dominance and ewe reproductive success, and between dominance and body size (Eccles & Shackleton 1986) may explain why there was no positive correlation between dominance and offspring sex ratio. If dominant ewes are not high-quality individuals, they should not produce more sons than subordinate ewes. There was no basis, however, to expect a negative correlation. In some primates, negative correlations between female dominance and offspring sex ratio have been found (Silk 1983; see Meikle et al. 1984 for opposite findings and conclusions). In these species the dominance rank of the mother has a greater effect on the reproductive success of daughters than of sons (Silk 1983), and in one captive population the cost of rearing daughters was greater for subordinate than dominant mothers (Gomendio et al. 1990). It seems unlikely that these scenarios apply to bighorn sheep. There are no differences in costs of sons and daughters

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according to maternal rank. There is no difference in fitness costs of sons and daughters, although sons are associated with increased parasite counts (Festa-Bianchet 1989b). Finally, there is no evidence that dominance status affects a ewe's relative ability to rear sons or daughters.

The negative correlation between offspring sex ratio and dominance does not have an obvious adaptive explanation and runs counter to the most widely accepted hypothesis for sex-ratio manipulation (Trivers & Willard 1973; Clutton-Brock et al. 1986). Post-hoc explanations are unwarranted, but the finding questions the generality of seemingly adaptive sex-ratio manipulations found in other species and merits further investigation.

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