

## **Social status in female bighorn sheep (*Ovis canadensis*): expression, development and reproductive correlates**

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**(With 4 figures in the text)**

Female bighorn sheep were studied over a 27-month period to quantify linearity and stability of social rank; expression of behaviour as a function of rank; development of rank relationships; and reproductive correlates of rank. Females exhibited a stable, non-linear hierarchy that correlated strongly with age. Dominant females used proportionally more threats, whereas subordinates used more subordination patterns. Females integrated into the hierarchy at 1–2 years of age and then fought their way to high social status. Dominant and subordinate females did not differ in pre-natal maternal investment, but dominant females nursed lambs at higher rates, and were more likely than subordinates to nurse alien lambs after their own lamb died.

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### **Introduction**

Social hierarchies are generally thought to allow priority of access to limited resources (e.g. mates, food) while reducing the risk of injury and permitting animals to exist in a more predictable social environment (Brown, 1975; Wilson, 1975). Although the concept of social dominance has been criticized (see Hand, 1986), it continues to be useful in the understanding of animal social systems.

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If high rank allows a female preferential access to resources, she may attain better body condition than subordinates, the benefits of which may be passed on to her offspring. Differences in body condition may result in differential sex ratios at birth and differences in maternal investment (Trivers & Willard, 1973; Clutton-Brock, Albon, & Guinness, 1984). Among ungulates, studies relating social status to reproductive fitness are rare, primarily because they entail long-term studies of recognizable individuals. Trivers & Willard (1973) hypothesized that females in better condition should invest more in, and produce more of, the offspring showing a higher variance in reproductive success. Clutton-Brock & Albon (1982) extended this argument: females in better condition should invest more in the more costly sex of offspring, provided that the effects of maternal investment are directly related to increases in reproductive success of those offspring. For most polygynous ungulates, male offspring are more costly to rear, and exhibit greater variance in lifetime reproductive success than female offspring. Dominant female red deer (*Cervus elaphus*), in better condition than subordinates, produced more male offspring and invested more in male offspring than did subordinates (Clutton-Brock, Albon & Guinness, 1986). However, female white-tailed deer (*Odocoileus virginianus*) and reindeer (*Rangifer tarandus*) in poor condition produced more male offspring (Skogland, 1986; Caley & Nudds, 1987; Verme, 1989). The relationship, then, between a female's social status, body condition and reproductive success is far from clear.

Prior studies on female ungulates have revealed that social status is correlated with age: red deer (M. J. Hall, 1983; Clutton-Brock *et al.*, 1984; Thouless & Guinness, 1986), white-tailed deer (Townsend & Bailey, 1981), ponies (*Equus caballus*: Clutton-Brock, Greenwood & Powell, 1976), reindeer (Espmark, 1964), roe deer (*Capreolus capreolus*: Espmark, 1974), bison (*Bison bison*: Rutberg, 1983, 1986). Among female cattle (*Bos taurus*), social status was highest for middle-aged females and lowest for young and old females (Reinhardt & Reinhardt, 1975; S. J. G. Hall, 1986). A few studies have revealed a positive relationship between social status and body condition (usually measured as body weight) in bison (in one habitat—see Lott & Galland, 1987—but not another—see Rutberg, 1983, 1986), reindeer (Kojola, 1989) and red deer (Clutton-Brock *et al.*, 1986). Only the studies on reindeer and red deer have related maternal investment to dominance status.

Bighorn sheep (*Ovis canadensis*) are highly polygynous ungulates in which male reproductive success is related to rank and fighting ability (Geist, 1971; Hogg, 1984, 1987). Males exhibit a highly linear hierarchy based on age (Hass & Jenni, 1991). A social hierarchy has not been demonstrated for free-ranging female bighorns, although captive bighorns do exhibit one (Bennett, 1986; Eccles & Shackleton, 1986). The objectives of this study were to investigate social status in a group of semi-captive female bighorn sheep over a 27-month period. The following questions were asked:

1. Does a linear hierarchy exist among female bighorn sheep, and how stable is it, year-to-year?
2. How are young animals integrated into the hierarchy?
3. How is social status reflected in interaction rates and types of behaviours used in interactions?
4. Does a female's social status influence pre- and post-natal maternal investment or offspring survivorship?

## Materials and methods

### *Study area and study population*

The study was conducted on the National Bison Range, a 75 km<sup>2</sup> National Wildlife Refuge in north-

western Montana. A 2.4-m high fence surrounds the Bison Range, preventing long-range dispersal. However, bighorns move freely within the boundaries and exhibit seasonal migratory patterns found in unconfined herds (Geist, 1971).

The bighorns on the Bison Range were descendants of 12 animals transplanted from Banff National Park, Alberta, during 1922. During this study the population contained 50–53 animals, including 27–30 females. All individuals could be recognized by unique horn characteristics. Ages of sheep were estimated by counting horn annuli, a task completed initially during 1980 by J. Hogg as part of another study (Hogg, 1984). Because ages of females > 4 years old cannot be reliably determined in the field (Geist, 1966), females 5 years of age or older during 1980 were classified as 'older'. Where ages were needed for calculations, a mean age was calculated for older females each year by assuming a yearly mortality rate of 11.7% (Geist, 1971) and a maximum age of 12 years. Ages of sheep born in 1980 and later were known precisely.

### *Data collection*

The study was conducted from June 1982 to September 1984. Female bighorn sheep were observed almost daily from June to early September each year. Observations centred on nursery groups composed of mature females, lambs and yearlings of both sexes. I approached to within 30 m of groups and wandered with them through the day. The rut began during November and daily searches for, and observations of, oestrous females were conducted until late December when most rutting activity ceased. Conception dates were considered to be the last day of oestrus, or were determined by backdating from the lambing date (about 174 days; Shackleton *et al.*, 1984). Lambing began in mid-May and intensive searches were conducted daily during 1983 and 1984 to find and capture new-born lambs for weighing and marking (total = 21 lambs; 43% of lambs born). Birthdate was determined from observing the birth or the lamb while it was still unsteady (< 24 h old), or from comparison with lambs of known age. Lamb sex was determined while the animal was being handled, or from observing urination postures (males stand, females squat). I observed the ruts of 1982 and 1983 and lambing of 1983 and 1984, and recorded nursing behaviour during the summers of 1982–1984. Dominance interactions were recorded intensively during the summers of 1982–1984 and opportunistically through the remainder of the year.

Observations of the nursery groups were conducted as follows: all-occurrences samples (Altmann, 1974) of nursing bouts were recorded for all lambs in view (Hass, 1990). If all members of a group could be consistently kept in sight (e.g. when bedded or grazing in an open area), all-occurrences samples of dominance behaviour were also recorded (total = 98 h). *Ad libitum* samples (Altmann, 1974) were recorded when group composition changed rapidly and during weekly censuses throughout the year (total = 537 h). Durations of all interactions were recorded to the nearest minute. During 1984, the behaviour patterns used in agonistic interactions were also recorded.

### *Assessment of social status*

Social status was determined by assembling a win-loss matrix (Brown, 1975) based on the outcome of agonistic interactions. Agonistic behaviours included butts, kicks and head-to-head clashes (contact patterns), low-stretches, threat jumps and horn threats (threat patterns), and face-rubbing (subordination pattern); behaviours described in Geist (1971). Contact and threat displacements from bedding sites, foraging locations, mineral licks, or other spatial locations were recorded as wins for the initiator, and face-rubbing was recorded as a win for the recipient. The winner of a dominance fight, involving a series of butts and clashes, was recorded as winning 1 interaction. Dominance matrices reflect status on 1 November each year. When both members of a dyad were observed dominating each other, the most recent winner of an interaction was considered dominant.

The degree of linearity of the hierarchies was calculated by Kendall's coefficient, *K* (Kendall, 1962; Appleby, 1983), using the win-loss matrices. The winner of the majority (> 50%) of encounters within a dyad was assigned a value of 1, and the loser received a value of 0. When relationships between 2 individuals were

unknown, Appleby (1983) suggested assigning an equal probability to each interactant. However, in this study, age was a large determinant of the outcome of interactions. Older females won 88% of encounters with younger females; when the relationship was unknown, older females were assigned a 0.88 probability of winning the interaction and younger animals a 0.12 probability. Females of equal age were each assigned 0.50. Values of Kendall's  $K$  range from 0 (non-linear) to 1.0 (completely linear). Values  $>0.90$  were considered representative of a linear hierarchy for this study. The coefficient  $K$  was used in preference to Landau's index of linearity,  $h$ , (Landau, 1951), owing to the lack of information in each of the matrices.

Dominance Values (Beilharz, Butcher & Freeman, 1966; Eccles & Shackleton, 1986) were calculated for females each year by using the win-loss matrices based only on recorded interactions (not including probabilities for unknown relationships). Dominance Values were used as relative measures of dominance, and were calculated by means of the arcsine transformation of the proportion of opponents dominated. Dominance Values ranged from 0.0 to 90.0 and were normally distributed, permitting the application of parametric statistics. Only animals interacting with at least 10% (arbitrarily chosen) of other herd members were ranked.

### *Development of rank relationships*

All-occurrences samples collected during 1983 and 1984 were used to determine if females of different ages interacted at different rates. Dominance interaction rates were obtained by dividing observed number of displacements by total hours of observation on each individual, averaged for all individuals in each age group. Rates were calculated separately for the number of displacements given and received. Proportions of different behaviours used in agonistic interactions were also compared for females of different ages and ranks.

### *Reproductive correlates*

The following variables were used to explore the relationship between social status and maternal investment: conception date, lamb's birth date, lamb survival to 6 months, lamb weight, lamb sex and nursing rate. In addition, it had previously been discovered that females on the Bison Range exhibited 3 types of maternal-care patterns—they nursed only their own lambs, they nursed their own and other lambs, or they nursed alien lambs after the death of their own lambs ('helpers'—Hass, 1990). Not all females that lost their lambs nursed alien lambs. Maternal-care pattern was also compared to social status.

### *Analysis*

For purposes of analysis, dominant females had Dominance Values above the median; subordinates, below the median. Age effects were separated from dominance effects by using either partial correlation (Sokal & Rohlf, 1981) or the index of Clutton-Brock *et al.* (1986) which ranks each animal within its cohort, then adjusts for the size of the cohort. Most females were observed in more than 1 year. Potential pseudoreplication (Machlis, Dodd & Fentress, 1985) was avoided by analysing years separately, or randomly deleting females so that they appeared only once in each data set. The structure of the hierarchies was tested by the  $\chi^2$ -test presented in Appleby (1983). Correlations were Pearson product-moment correlations. Proportions of behaviours used in agonistic interactions were transformed by means of the arcsine transformation. Conception and birth dates were skewed toward the beginning and were tested with the Mann-Whitney  $U$ -statistic (Sokal & Rohlf, 1981). Nursing rates declined with lamb age. Average nursing rates of dominant females were compared pair-wise to those of subordinate females, according to the age of their lambs, using the Wilcoxon signed-ranks statistic,  $T$  (Sokal & Rohlf, 1981). Tests were 2-tailed unless otherwise noted. Probabilities of  $<0.05$  were considered significant except in the case of multiple comparisons when  $\alpha$  was adjusted for the number of comparisons (Sokal & Rohlf, 1981: 241).

### Structure of the hierarchies

Each year at least two females were not observed interacting and could not be ranked. Females usually associated with the nursery group for their first few years. Non-lactating females four years of age and older associated in unstable groups of 2–5 animals; these females occasionally joined the nursery group for short periods of time. Non-lactating females older than seven years seldom joined the nursery group; they spent much of their time alone or in the company of one or two other females. All but one of the females not included in the hierarchy fell into this latter category. The percentage of dyads observed interacting ranged from 28% to 74% (Tables I–III). Results of the win-loss matrices revealed hierarchies that were not linear, but were significantly non-random (1982:  $K=0.66$ ,  $\chi^2=190.96$ ,  $P<0.001$ ; 1983:  $K=0.77$ ,  $\chi^2=221.39$ ,  $P<0.001$ ; 1984:  $K=0.66$ ,  $\chi^2=232.70$ ,  $P<0.001$ ). Dominance Values were correlated significantly with age (1982:  $r=0.87$ ,  $d.f.=18$ ,  $P<0.01$ ; 1983:  $r=0.73$ ,  $d.f.=22$ ,  $P<0.01$ ; 1984:  $r=0.74$ ,  $d.f.=26$ ,  $P<0.01$ ). Dominance Values were highly correlated year-to-year, indicating considerable stability (1982–1983:  $r=0.81$ ,  $d.f.=19$ ,  $P<0.01$ ; 1983–1984:  $r=0.78$ ,  $d.f.=22$ ,  $P<0.01$ ; 1982–1984:  $r=0.69$ ,  $d.f.=22$ ,  $P<0.01$ ). More than 80% of observed interactions were displacements, of which 97–99% were from bedding sites and spatial positions. Less than 1% were from feeding sites (Table IV).

*Win-loss matrix, Dominance Values (D.V.) and ages for female bighorn sheep during 1982. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting = 28%; number of interactions = 172. + = females  $\geq$  five years old during 1980. Not included here are one 2-year-old and six 7+-year-old females that were not ranked*

D.V.	Age (years)	Individual																								
		15	17	21	06	08	01	10	22	02	11	05	16	12	09	26	25	29	27	28	24					
90.0	7+	15	—	4		7			1	1		3		4	1	1	2	2	9	2	5					
90.0	7+	17		—	3	1					1	2		5	1				2	1	1					
69.7	7+	21		—		2		1	1	1	1	1	1	1	1	3		1	3	2	1					
68.0	5	06			—				1					3		1			1	1	1					
61.3	6	08			1	—	1		2	3	2	1		1	1	2	2		6	4						
54.9	6	01					—									1		1								
54.9	4	10						—				2							1							
54.9	6	22							—	2	1	2		1		2			1	2	3					
53.1	3	02								—		1	2	1	4	1			1							
51.9	5	11				1					—			1		1			1		1					
38.1	2	05										—						1	1	2	1	1				
35.1	5	16											—								1					
35.1	2	12										5		—				1	1	1						
32.6	2	09													—			1			1					
31.3	2	26														—		1	1		1					
20.3	1	25																—			1					
20.3	1	29																	—		1					
16.4	1	27																		—		1				
16.4	1	28																			—	3				
00.0	1	24																				—				

TABLE II

Win-loss matrix, Dominance Values (D.V.) and ages for female bighorn sheep during 1983. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting = 74%; number of interactions = 472. + = female  $\geq 5$  years old during 1980. Not included here are three 8+-year-old females that were not ranked

D.V.	Age (years)	Individual																											
		15	14	11	17	02	21	13	04	01	08	18	06	10	16	09	12	05	26	25	27	29	22	24	28				
77-0	8+	15	—			11	13	4	1	7	2	1	1	3	1	1		2	2	1	7	2	2	3	3				
70-6	8+	14	3	—			8	12		4		4	1	1	2	1	3		1		4	2	10	6	1				
70-6	6	11			—						4	3			1			1			1	1	1		2				
65-5	8+	17						2							1	2							1	1					
64-2	4	02		4		1	—	4		10		1	1	1	1	2	1	1	2		4	8	1	1	1				
60-7	8+	21						7			1	1	1		1	1	5		1	2	7	2	4	4					
60-7	8+	13			1	3				3	2	2	1			4	1		2		2		1	3	1				
60-0	8+	04				1			—	1			3																
56-8	7	01					16			—		2	2	5	2	2	1	2	4	1	10		10	4	3				
56-2	7	08				5				1	—			2				1	2	1		1	1		1				
48-2	3	18										—			1	1	3		2	2	3	3	2	4	1				
46-7	6	06										—		2		2	1		1	1	1			4	1				
41-6	5	10										5		—			6	1	1		7	2		4	3				
38-1	6	16											1	—			2						1						
36-9	3	09												1	2	—			1	1			1						
36-9	3	12									1						—		5	2	1		2	10					
33-2	3	05																—			1		1	1					
32-6	3	26												2		2	2		—			1	2						
31-3	2	25																		—	1		1	1					
28-7	2	27																			—		1	1	1				
24-4	2	29																				—	1	1	1				
15-3	7	22																					—	1	1				
14-2	2	24																						—	1	1			
14-2	2	28																						7	—				

### Development of rank relationships

Female bighorn sheep increased most rapidly in status from 1–4 years of age, but continued to gain in rank until at least nine years old (Fig. 1). Interaction rates also changed with age; the rates at which females displaced others increased with age, whereas rates at which individuals were displaced generally decreased with increasing age (Fig. 2). Both rates peaked for females of 4–5 years of age. The proportion of threats used in agonistic interactions increased with increasing rank, and the proportion of subordination displays decreased (Fig. 3). Changes in threats were related more closely to dominance than age; changes in subordination behaviour were related more closely to age (Table V).

During the study, nine dominance fights were observed between females, of which five resulted in changes in the relationship between the females involved. An additional 21 changes in dyadic relationships were detected from dominance interactions, but without seeing actual fights. Most changes (58%) were the results of three- and four-year-olds advancing in the hierarchy. The lowest ranking females generally were the yearlings and two-year-olds (Tables I–III). Agonistic interactions were very rare among lambs and no evidence of dominance relationships was apparent (Hass, 1986). Yearlings seldom interacted among themselves, and relationships among them were difficult to determine. By two years of age, clear-cut dominance relationships were



TABLE IV

*Number of displacements at different locations by female bighorn sheep on the National Bison Range. Percentages in parentheses*

Year	Locations					Total
	Bedding sites	Spatial positions	Mineral licks	Horning posts	Feeding sites	
1982	108 (68)	50 (31)	1 (<1)	1 (<1)	0	160
1983	277 (63)	154 (35)	2 (<1)	4 (1)	2 (<1)	439
1984	330 (59)	213 (38)	11 (2)	4 (<1)	2 (<1)	560

evident. By 3–4 years of age, females actively fought their way up the hierarchy, making it possible for a four-year-old to be highly ranked. Although variability in Dominance Values increased among older females, they did not appear to lose rank with increasing age.

### *Reproductive correlates*

No differences were found in the conception dates of dominant and subordinate females (1982:  $U = 70$ ,  $n = 10, 10$ ,  $P > 0.05$ ; 1983:  $U = 69$ ,  $n = 11, 12$ ,  $P > 0.05$ , Table VI). Likewise, there were no differences in birth dates of lambs born to dominant and subordinate females (1983:  $U = 42.5$ ,  $n = 10, 10$ ,  $P > 0.05$ ; 1984:  $U = 49.5$ ,  $n = 11, 11$ ,  $P > 0.05$ , Table VI). Females that nursed a male lamb conceived significantly later ( $17 \text{ December} \pm 11.5 \text{ days}$ , not counting helpers) than females that nursed female lambs ( $2 \text{ December} \pm 2.9 \text{ days}$ ,  $U = 16$ ,  $n = 4, 4$ ,  $P = 0.025$ , one-tailed test) or females that did not nurse a lamb ( $3 \text{ December} \pm 9.6 \text{ days}$ ,  $U = 64$ ,  $n = 4, 19$ ,  $P < 0.025$ ). There were no differences between conception dates of non-lactating females and those of females nursing female lambs ( $U = 39$ ,  $n = 4, 19$ ,  $P > 0.10$ ). Sex of previous lamb and dominance status together accounted for 98% of the variance in conception dates.

Very high lamb mortality ( $> 75\%$ ) was observed on the Bison Range during 1982–1984, due mostly to predation (Hass, 1989). Two lambs survived during 1982, and six during 1983. During

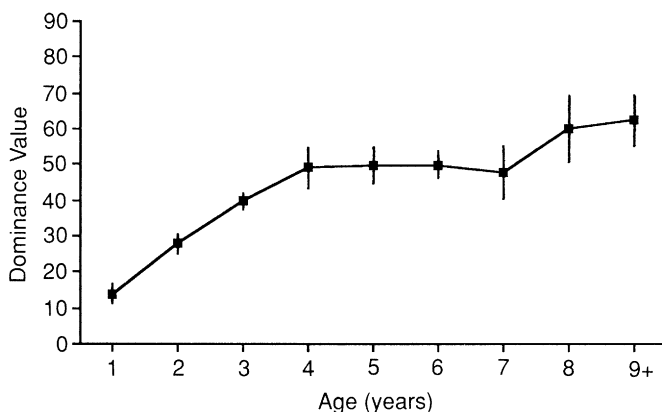


FIG. 1. Mean ( $\pm$ S.E.) Dominance Values for female bighorn sheep on the National Bison Range, 1982–1984. Some individual females are represented in more than one age group.



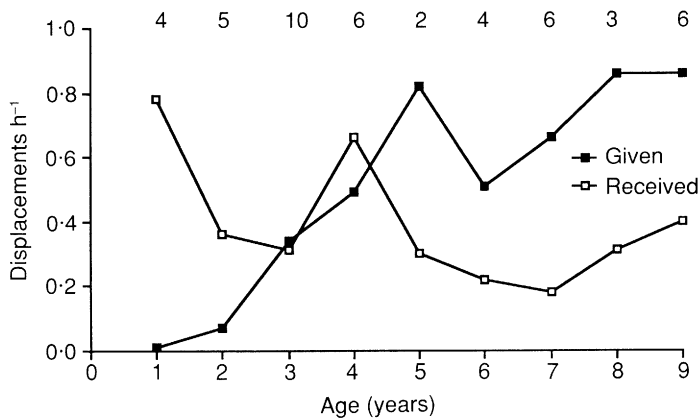


FIG. 2. Mean displacement rates for female bighorn sheep on the National Bison Range, 1983 and 1984 combined. Numbers across the top refer to the number of females in each age group. Some individuals are represented in more than one age group.

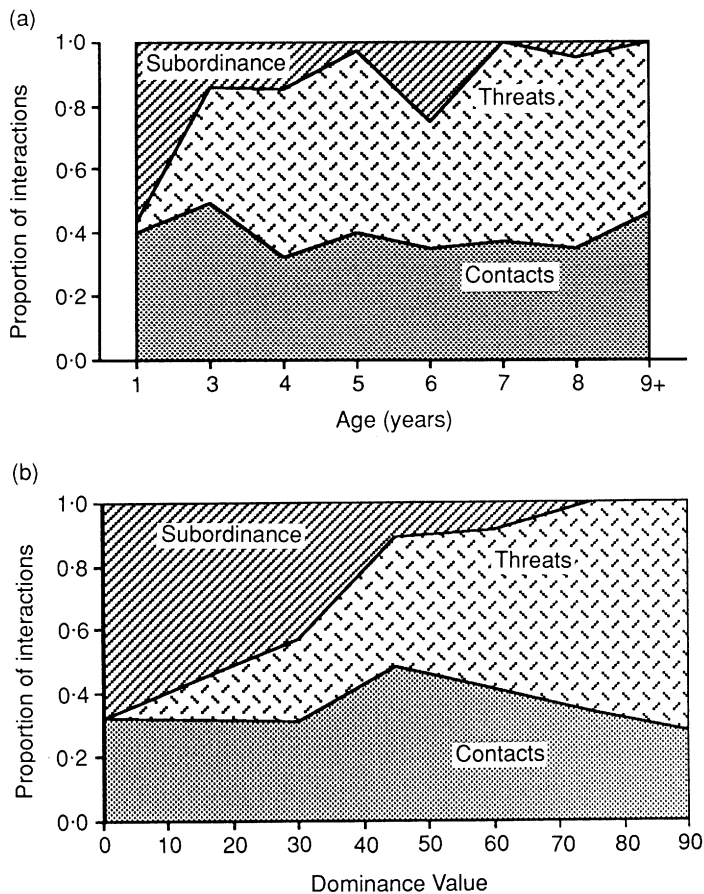


FIG. 3. Proportion of subordination, threat and contact behaviours performed by female bighorn sheep during 1984, by (a) age and (b) Dominance Value.

TABLE V

*Partial correlation coefficients for contact, threat and subordination behaviours performed by female bighorn sheep on the National Bison Range during 1984, controlling the effects of age and rank. \*\*Significant at  $\alpha=0.025$*

	Contact	Threat	Subordination
$r$ rank·age	0.02	0.51**	-0.37
$r$ age·rank	0.02	0.26	-0.43**
Multiple $R^2$	0.33	0.93	0.84
$F$	6.22**	154.55**	66.95**
$N$	28	28	28

1984, two lambs survived to four months, but only one to six months. Although most of the surviving lambs were born to dominant females (Table VI), differences were not significant (Fisher's exact test, 1983:  $P=0.50$ ; 1984:  $P=0.50$ ). Sex ratios at birth did not differ between dominant and subordinate females (Fisher's exact test,  $P>0.20$  for both dominant and subordinate females; Table VI).

Lamb weights did not differ between lambs that died and lambs that survived (Hass, 1989). No relationship was found between weights of lambs born to dominant and subordinate mothers for male lambs ( $t=0.62$ ,  $d.f.=9$ ,  $P>0.05$ ), female lambs ( $t=0.95$ ,  $d.f.=5$ ,  $P>0.05$ ) or both sexes together ( $t=0.11$ ,  $d.f.=16$ ,  $P>0.05$ ; Table VI).

Females that lost their lambs but continued to nurse alien lambs (helpers) had significantly higher Dominance Values ( $\bar{x} \pm \text{S.D.} = 67.5 \pm 11.07$ ,  $n=7$ ) than females that still had their lambs

TABLE VI

*Summary of reproductive data for dominant and subordinate female bighorn sheep on the National Bison Range, 1982-1984*

	Dominants	Subordinates
Percentage conceiving before median conception date ( $n$ )		
1982	50 (10)	50 (10)
1983	55 (11)	64 (11)
Percentage giving birth before median lambing date ( $n$ )		
1983	50 (10)	50 (10)
1984	45 (10)	55 (11)
Mean ( $\pm$ S.D.) lamb weights, kg ( $n$ )*		
Male	4.1 $\pm$ 1.00 (6)	4.3 $\pm$ 0.37 (5)
Female	4.4 $\pm$ 0.10 (3)	3.9 $\pm$ 0.95 (4)
Both	4.2 $\pm$ 0.81 (9)	4.1 $\pm$ 0.68 (9)
Percentage lamb survival to females > one year old ( $n$ born) <sup>a</sup>		
1983	25 (12)	25 (12)
1984	7 (14)	0 (8)
Lamb sex ratio at birth, males: females (% male) <sup>a</sup>	10:6 (63)	6:7 (46)
Percentage nursing alien lambs after own lamb died ( $n$ born) <sup>a</sup>		
1983	17 (12)	0 (12)
1984	29 (14)	0 (8)

<sup>a</sup> Does not include three lambs born to females that were not ranked

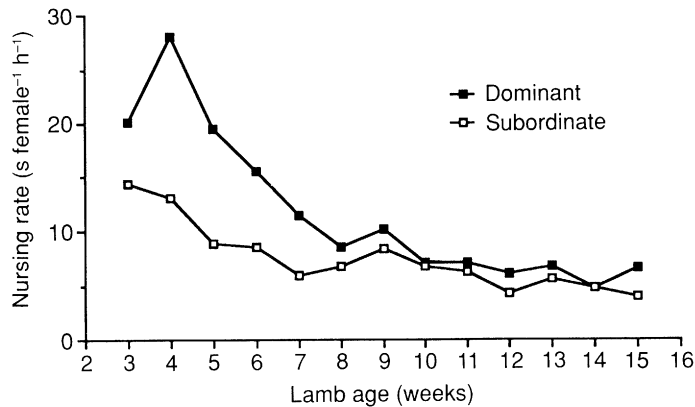


FIG. 4. Nursing rates of dominant and subordinate female bighorn sheep on the National Bison Range, 1983 and 1984 combined.

( $48.3 \pm 16.57$ ,  $n=8$ ,  $t=2.59$ ,  $P<0.05$ ). Mean Dominance Values of females that nursed only their own lambs did not differ from those of females that nursed their own and alien lambs ( $t=0.63$ ,  $d.f.=6$ ,  $P>0.40$ ). Seventeen to 29% of dominant mothers became helpers following the death of their lambs; none of the subordinates did (Table VI).

Dominant females nursed lambs at significantly higher rates than did subordinate females (helpers excluded, Wilcoxon signed-ranks,  $T=0$ ,  $n=13$ ,  $P<0.001$ ; Fig. 4). This difference persisted when age effects were removed ( $T=19.5$ ,  $n=13$ ,  $P<0.05$ ). Although nursing rates did not differ among years, suckling rates did (owing to additional nursing by helpers: Hass, 1990). Only during 1983 were surviving male and female lambs present. During this year, suckling rates did not differ between sexes ( $T=32$ ,  $n=12$ ,  $P>0.05$ ). Whether dominant and subordinate females nursed male or female lambs at different rates could not be determined because all surviving male lambs ( $n=4$ ) were born to dominant females.

## Discussion

### *Structure and development of dominance relations*

A stable, age-related hierarchy was evident for female bighorn sheep on the Bison Range. A large number of triangles, in which individuals are dominated by individuals of lower rank, were apparent in this group. Dominance relationships probably did not exist at a higher level than individual dyads. Female bighorn sheep reach most of their body and horn size at 2–3 years of age (Blood, Flook & Wishart, 1970; Jorgenson & Wishart, 1984). During each year, at least 12 ranked females were aged three years and older, and the more females in this category, the greater the number of triangles in the ranks. Other studies of ungulates have found similar results: numerous triangles in isomorphic groups of more than 10 animals (Beilharz & Mylrea, 1963; Espmark, 1964; Clutton-Brock *et al.*, 1976; Collis, 1976; S. J. G. Hall, 1986; Rutberg, 1986). An ordinal ranking system also resulted in numerous triangles among the females (C. C. Hass, unpubl. data). A cardinal ranking system, such as the calculated Dominance Values, was believed to describe more accurately relationships among the female bighorn sheep in this study.

For the first couple of years, females advanced in status by default, as younger females joined the bottom of the hierarchy. At 3–4 years of age they began actively fighting their way up the ranks. As females got older, they displaced other females at higher rates, but this may have been a function of the number of subordinates available for them to displace. The types of behaviours used in interactions changed; the proportion of threats performed appeared to change as a function of rank, while the proportion of subordination patterns appeared to change with age. Geist (1971) suggested that female bighorn sheep stopped maturing behaviourally when they reached sexual maturity. This study does not support that contention; females in this herd matured sexually at 1.5 years of age, but did not appear to act as 'adults' until 4–5 years of age. It was at this age that the proportion of threats became greater than the proportion of contact patterns used in agonistic interactions, and that females interacted at the highest rates.

Rutberg (1986) and Thouless & Guinness (1986) suggested that older females 'teach' younger females to behave subordinately, thus accounting for the age-dominance relationship and the rarity of escalated aggression among female bison and red deer. However, female bighorn sheep in this study fought relatively frequently, and actively fought their way up the hierarchy. The number of fights observed during this study implies that there may be some real benefits to high rank. Perhaps the costs of fighting are less for female bighorn sheep than for female bison and red deer.

Displays are less costly physiologically to bighorns than contact patterns (MacArthur, Geist & Johnston, 1982); and high-ranking females used displays (threats) more often than contact patterns to displace other females. At the Denver Zoo, high-ranking females performed displays more often than did low-ranking females (Bennett, 1986). However, in another captive herd, Eccles & Shackleton (1986) found that females performed contact patterns more than displays.

### *Reproductive correlates of rank*

Of all the reproductive variables measured during this study, only two appeared related to social status: nursing rate and maternal-care pattern. No relationship was found between measures of pre-natal maternal investment (lamb weight, lamb sex or lamb birth date) and social status. Female bighorn sheep on the Bison Range were generally in excellent condition: they matured sexually at a young age relative to other populations (Geist, 1971), most females produced lambs every year, and they did not appear to be forage-limited (Hass, 1990). Low lamb survivorship was due primarily to predation (Hass, 1989). Social status would not be expected to affect lamb survival in the same way as if food were limited and maternal status influenced access to food or protected young from the effects of competition. Experience gained with age and previous exposure to predators might result in older females losing fewer offspring to predators; however, in this study, ages of females whose lambs died did not differ from ages of those whose lambs survived (Hass, 1989).

Females may have been able to invest maximally in lambs pre-natally regardless of social status. In food-limited populations, differences in body condition between dominant and subordinate females may be more pronounced and may result in differences in pre-natal investment. Although conception dates (and subsequent birth dates) were later following the nursing of a male lamb, birth dates did not affect lamb survival in this herd (Hass, 1989) as they do in other herds (Festa-Bianchet, 1988a).

Lactation produces a much greater strain physiologically than does gestation (Oftedal, 1985; Clutton-Brock, Albon & Guinness, 1989). Dominant females nursed their own lambs at higher rates, and some became helpers, aiding in the survival of relatives within the herd (Hass, 1990).

This may support the idea that dominant females were in better body condition than subordinates. Although precise locations of interactions were not recorded, most consisted of females displacing each other from bedding sites in the shade during hot (32–41 °C) afternoons. Perhaps by reducing thermal stress dominant females were able to maintain better body condition.

Females that nursed male lambs conceived significantly later during the following breeding season than females that nursed female lambs or were not lactating, indicating that male lambs may have been more costly to rear. Male lambs grow at a faster rate (Jorgenson & Wishart, 1984). Nursing rates did not differ between the sexes, but sample sizes were small. Festa-Bianchet (1988*b*) found that male bighorn lambs suckled for shorter periods than female lambs. Among Dall sheep (*Ovis dalli*), a female's body condition during gestation and lactation affected horn growth of her male lamb for up to five years after birth, but affected her female lamb to a lesser extent (Bunnell, 1978). Horn size is an important component of fighting ability for male mountain sheep (Geist, 1971). Although no studies have linked horn size to male reproductive success, I suggest that maternal investment by a female mountain sheep may influence the reproductive success of her sons more than her daughters, and that this influence probably is dependant on a female's age and/or social status. In this study, dominant females invested more in their offspring, post-natally, than did subordinates. Further studies may reveal sex differences in post-natal maternal investment, which in turn may be affected by maternal dominance status. Bighorn sheep inhabit a variety of habitats which result in differences in the timing and durations of lambing seasons (Geist, 1971; Turner & Hansen, 1980) and differences in post-natal maternal investment patterns (Hass, 1990). Different environments, with resulting differences in diet quality, and predation or parasite levels, may produce very different effects of social status on female reproductive success.

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