

Social dominance in adult female mountain goats

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Abstract. The social behaviour of adult female mountain goats, *Oreamnos americanus*, was studied for 2 years in an un hunted population in west-central Alberta, Canada. Compared with other female ungulates, mountain goat females interacted aggressively much more frequently and their dominance ranks were less stable in time and less age-related. Goats were organized in a non-linear but non-random dominance hierarchy, with many reversals in rank. The best morphological predictor of dominance rank was horn length one year and body mass in the following year. Age was a weaker predictor of dominance status than what has been reported for other female ungulates. The ranks of individual goats changed between years and dominance rank one year was not a good predictor of rank the following year. These results suggest that linearity may only be possible when a contested resource can be defended. Dominant female goats did not forage more efficiently than subordinate goats, and dominant status did not affect the amount of time devoted to alert behaviour.

Two major ecological pressures affect the evolution of sociality; predation and the distribution of resources (Alexander 1974). For mountain ungulates, sociality may be an anti-predator strategy, because they exploit open environments where they are vulnerable to predation and rely on alertness and proximity to escape terrain to avoid being caught (Hamilton 1971; Wilson 1975; Festa-Bianchet 1991).

Sociality includes potential costs as well as benefits. The major potential drawbacks of group-living include an increased probability of transmission of disease or parasites (Hoogland 1978; but see Hart & Hart 1992; Arnold & Lichtenstein 1993), competition for food or mates with other group members (Barrette & Vandal 1986) and the need to defend an individual space. Competition may lead to intraspecific aggression within groups and individuals may benefit from patterns of social behaviour that allow them to avoid the costs of aggression. One such mechanism is social dominance.

Social dominance may limit the costs of aggression by limiting interactions to threats as opposed to physical contacts (Archer 1988). For this paper, social dominance is defined as the relationship between two individuals, where one (the subordinate) predictably yields to the other (the dominant) during interactions (Kaufmann 1983).

An interaction is defined as an encounter between two individuals that results in the loser (the subordinate) backing away from the winner (the dominant).

It has been suggested that when a social dominance hierarchy is established within a group, the outcome of subsequent aggressive interactions is predictable from previous encounters (Rowell 1974). Two major functions have been proposed for social dominance. First, it may allow dominant individuals priority of access to a limited resource (Kaufmann 1983). Second, it may reduce the level of aggression in a group: this may benefit individual animals because they will avoid potentially costly interactions with conspecifics, whether dominant or subordinate (Rowell 1974; Bernstein 1981). A subordinate would benefit by not challenging a dominant over some resource because if it interacted with the dominant it would probably not obtain the resource and risk injury. A dominant would benefit by not having to re-establish its superiority over the subordinate at each new contact, which would involve some energetic cost and some risk of injury. Risk of injury would be a very important factor in the behaviour of animals that possess dangerous weapons such as sharp horns, claws or teeth.

The ultimate benefits of dominance, such as increased fitness, are the same for males and

females but the proximate benefits may differ. For most male mammals, the proximate advantage to dominance is that dominant status allows access to oestrous females (Emlen & Oring 1977). For females, on the other hand, dominance usually ensures priority of access to a food resource. If dominance status guarantees priority of access to food, dominant individuals could benefit from increased foraging efficiency through better growth, better survival and ultimately greater reproductive success than subordinates. Higher foraging efficiency, but not reproductive success, has been shown to be associated with dominance for several female ungulates, such as woodland caribou, *Rangifer tarandus* (Barrette & Vandal 1986) and bison, *Bison bison* (Rutberg 1986). A correlation between female dominance status and reproductive success, however, has only been shown for red deer, *Cervus elaphus* (Clutton-Brock et al. 1986). Several studies of bighorn sheep, *Ovis canadensis*, have repeatedly failed to show any link between female dominance and reproductive success (Eccles and Shackleton 1986; Festa-Bianchet 1991; Hass 1991).

The social system of the mountain goat, *Oreamnos americanus*, is characterized by dominance-subordination relationships (Chadwick 1977). Outside the rut, adult females are dominant to all other sex-age classes. This system should favour a more predictable social environment, thus reducing the risk of injury and also lowering energy expenditures through diminished fighting. Reduction in aggression would be very profitable to individuals in this species because these animals possess horns that can injure or kill conspecifics (Geist 1964, 1967; personal observation). If dominance limited aggression to threats and provided a predictable social environment, rates of aggression should be low because rank would be respected. Most studies of ungulates have found that females are not very aggressive to each other, and have suggested that there are normally no resources that would justify the risks inherent in challenging an individual against whom a female may have already lost once (Thouless & Guinness 1986; Festa-Bianchet 1991). We expected to find similar results for mountain goats.

The objectives of this study were to characterize social dominance relationships between adult females. More specifically, we wanted to determine how often goats interacted aggressively, and

if they exhibited a dominance hierarchy with stable social relationships. Second, we searched for the best predictor(s) of social status. Other studies of female ungulates suggest that age should be very important (Thouless 1990; Festa-Bianchet 1991; Locati & Lovari 1991), but body or horn size may also play a role (Rutberg & Greenberg 1990), or reproductive status (presence or absence of a nursing kid) if aggression was mostly used to defend offspring (Green et al. 1989; Maestripietri 1992). Finally, we wanted to determine whether dominant individuals gained a direct advantage through increased foraging efficiency (Lovari & Rosto 1985).

METHODS

Study Area and Population

The study was conducted at Caw Ridge, Alberta (54°N, 119°W), a rolling mountain complex (1750–2150 m in elevation) consisting of four major peaks. The goats use approximately 21 km² of alpine and subalpine habitat, characterized by forbs and grasses. The study area is a front range of the Rocky Mountains, and is separated from the main mountain range by approximately 30 km of coniferous forest. Goat hunting on this site has been prohibited since 1969.

A capture programme was initiated in 1989 to mark individuals for easy identification in the field. Goats were captured with two remote-controlled box traps and four self-releasing traps baited with salt. Captured adult goats were drugged via an intramuscular injection of xylazine which was later reversed by an injection of idazoxan (Jorgenson et al. 1990). Kids and yearlings were not drugged. Captured goats were measured and weighed, then fitted with either plastic ear tags or canvas collars. Twelve and 13 adult female goats also had radio collars in 1991 and 1992, respectively. Goats were located daily, visually or by radio telemetry, between late May and early September 1991 and 1992. Marked individuals were identified and unmarked goats were classified by sex and age according to Smith (1988). The reproductive status of adult females (≥ 3 years) was determined either at capture or during observations (whether or not seen nursing a kid). We are confident that our population estimates were within one to two individuals of the actual number because we consistently saw the

same number of marked and unmarked goats of different sex-age classes during daily censuses of the nursery group and weekly censuses of males in the study area. The nursery group included adult females, kids and juveniles.

Behavioural Data Collection

We observed goats with a 15–45 × spotting scope or 15 × 60 binoculars. During summer, adult males (≥ 3 years) are spatially segregated from the nursery herd, the latter being the focus of this study. We measured time budgets and agonistic interactions of adult females using 1-h focal-animal sampling (Altmann 1974). In addition to registering agonistic interactions for focal animals, we noted agonistic interactions occurring between marked individuals in the group using all-occurrence sampling (Altmann 1974). All interactions seen were used to assess dominance relationships among adult females.

Foraging efficiency was defined as the proportion of time a goat spent feeding while active (Owen-Smith 1979). To minimize the chance of a biased estimate of the percentage of time spent feeding, we only used data for goats that were active for a minimum of 20 min during focal samples. This procedure eliminated goats that were only active for a few minutes and could have spent those minutes feeding exclusively or moving to a foraging site. The remaining patterns of behaviour in the time budget were: alert (head upright, scanning the surroundings), bedded (often ruminating) and 'other' (standing, travelling).

Dominance Relationships

We determined dominance ranks by assembling win-loss matrices based on the outcomes of agonistic interactions between adult females. Win-loss matrices are often ordered in a way to minimize the number of interactions below a diagonal line (Schein & Fohrman 1955). Appleby (1983), however, suggested that such a procedure could obscure irregularities in the hierarchy by increasing the overall impression of linearity. In our study we used the same classification as Barrette & Vandal (1986). We ranked individuals according to the following ratio of wins versus losses: $\text{Rank} = \text{Wins} + 1 / \text{Losses} + 1$; the highest ratios indicating superior ranks. We then ordered

the animals according to their ratios. This procedure gave us an impression of an individual's overall dominance status or ranking in the group. We compared our method of calculating the dominance rank with another method (Eccles & Shackleton 1986; Hass 1991) to determine the reliability of our calculation of ranks compared with other studies. This second method consists of calculating an individual's dominance value according to the proportion of opponents dominated ($DV = \arcsin \sqrt{x}$, where x is equal to the proportion of opponents dominated). We decided to use our measure of dominance because the correlations between our ranks and those calculated from the dominance values were very strong ($r = 0.97$ in both years). We then measured the linearity and the transitivity of the dominance hierarchy.

We used Kendall's coefficient, K (Appleby 1983), using the win-loss matrices to measure the linearity of the hierarchy based upon dominance ranks. Values of Kendall's coefficient range from 0 (complete absence of linearity) to 1 (complete linearity). The individual that won the majority (more than 50%) of interactions within a dyad was assigned a value of 1 whereas the loser received a value of 0. Appleby (1983) suggested that both individuals should be assigned a value of 0.5 in unknown relationships (blank cells in the matrix) stating that they have an equal opportunity of winning. Since age was presumed to be an important factor determining dominance rank, we followed the methodology outlined in Hass (1991) which factors in this age effect.

Older females won 66% and 69% of interactions in 1991 and 1992, respectively. When relationships in 1991 were unknown, the older female was assigned a 0.66 probability of winning the encounter and the younger female a 0.34 probability. Females of equal age were both assigned a value of 0.5. The same calculations were done for the 1992 data using probabilities of 0.69 for older females and 0.31 for younger females. A hierarchy was considered linear if K was greater than or equal to 0.9; this value of K was also used by Hass (1991) in her study of bighorn ewes. Arranging a win-loss matrix into a specific order may create linear relationships where no such relationships exist, so the structure of the hierarchy was tested using the chi-squared test presented in Appleby (1983). This test measures the probability of the hierarchy occurring by chance.

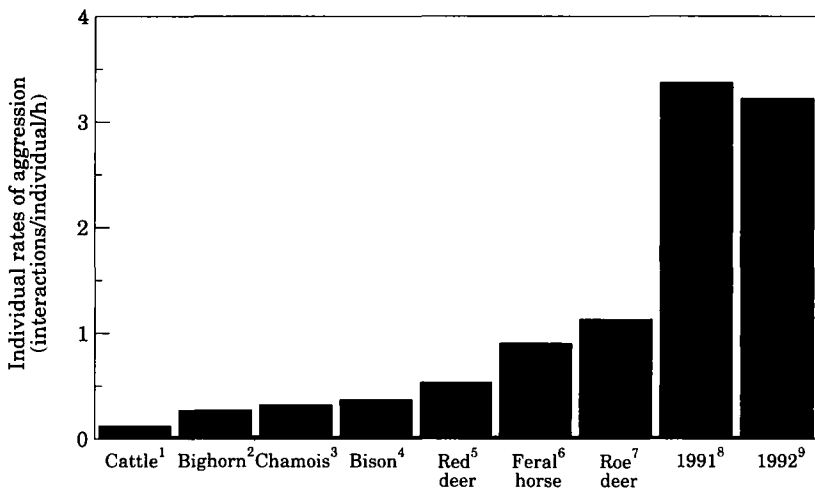


Figure 1. Hourly rates of aggressive behaviour among female ungulates (1: Clutton-Brock et al. 1976; 2: Hass 1986; 3: Locati & Lovari 1990; 4: Rutberg 1986; 5: Thouless 1990; 6: Rutberg & Greenberg 1990; 7: Espmark 1974; 8 and 9: mountain goats, this study).

We calculated two measures of the stability of dominance ranks from our data: reversals and intransitivity. Within dyads (two individuals), reversals were defined as interactions in which a subordinate individual defeated an individual ranked higher in the hierarchy. Dominance hierarchies are said to be linear when all interactions are transitive (Appleby 1983). Transitivity exists where A dominates B, B dominates C and A dominates C. A relationship is intransitive when these conditions are not met. We calculated the number of intransitive triads (three individuals) among all possible triads in both years of the study. These analyses permitted us to test the influence of reversals and intransitivities on the stability of dominance ranks.

To assess the influence of morphometric traits on dominance rank, we compared body mass and horn lengths of captured adult females with dominance rank each year. Measurements were only available for eight females in 1991 and seven females in 1992.

We tested the stability of dominance hierarchies and the value of several potential dominance indicators as predictors of dominance rank with linear regression. We used a *t*-test to determine whether lactation affected dominance rank. A non-parametric ANOVA was used to verify whether there was a relationship between time budget and dominance status. All results refer to individual goats and not to focal samples. Because

individuals contributed repeated observations to the data set, we used averages for statistical procedures. All statistical tests were two-tailed, and probability values less than or equal to 0.05 were considered statistically significant. All analyses were carried out with the Statview package for Macintosh (Abacus Concepts, Berkeley, California).

RESULTS

Intraspecific aggression is an integral part of mountain goat sociality as reflected in the 1168 agonistic encounters between goats noted in 315 h of observations of the nursery group for both years combined. Of all these interactions between members of the nursery group, only those occurring between marked adult females were used to examine dominance relationships (1991: 122 interactions; 1992: 305 interactions). Agonistic interactions consisted mainly of displacements (99%) at resting or feeding sites, where one female approached and displaced another female without contact. Rushes and horn threats accounted for the remainder of the interactions. Mountain goats appear to have a much higher rate of aggressive interactions than other gregarious female ungulates (Fig. 1).

Win-loss matrices for interactions among adult females revealed dominance hierarchies for both

Age (years)	16	57	42	41	15	7	71	34	60	68	63	31	50	86	8	73	59	49	54	46	84
7	16		*	**	***	**		***	*			*	**	*		**		*		*	*
7	57	*					*	**				*			*	*	*	**	*	*	*
9	42								***			**		*	*	*	*	*	*	*	*
9	41					*		*						**			****	*	*	*	*
8	15			**				**						*					*	*	*
8	7						*							*		*	*	*	*	*	*
6	71								*	*	*		*	*	*	*	*	*	*	*	*
9	34							*	*	*	*	**	**	**	**	*	*	*	*	*	*
7	60								*	**	*		*	*	**	*	*	*	*	*	*
3	68										**	*				*	*	*	*	*	*
5	63	*						*	*	*	*	*	*	*	*	*	*	*	*	*	*
4	31					*		*	*	*	*	*	*	*	*	*	*	*	*	*	****
4	50					*		*	*	*	*	*	*	*	*	*	*	**	*	*	*
5	86															*	*	*	*	*	*
7	8														**	**	**	**	*	*	**
6	73											*	*	*	*	*	*	*	*	*	*
5	59										**	*	*	*	*	*	*	*	*	*	*
6	49							*	*	*	*	*	*	*	*	*	*	*	*	*	*
6	54									*	*	*	*	*	*	*	*	*	*	*	*
3	46																				*
3	84																				*

Figure 2. Win-loss matrix for adult female mountain goats, Caw Ridge, Alberta, 1991. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting: 40%. Number of interactions: 122.

years, and these hierarchies were non-linear but significantly non-random (1991: $K=0.57$, $\chi^2=105.9$, $df=36$, $P<0.001$; 1992: $K=0.46$, $\chi^2=162.2$, $df=28$, $P<0.001$). The coefficient of linearity can be influenced by reversals in rank and also by the number of unknown relationships in the hierarchy as indicated by blank cells (Appleby 1983; Figs 2, 3). The low values of K in both years are probably due in part to the number of missing cells in the win-loss matrices.

In 1991, interactions were seen for 83 of 210 possible dyads (40%), and in 1992, 193 of 435 possible dyads (44%) were seen to interact. In both years there was an approximately equal proportion of dyadic reversals in rank (1991: 15 reversals, 12% of total interactions; 1992: 47 reversals, 14% of total). In 1991, 53% of the reversals were the result of younger females defeating older ones; the difference in age was less than or equal to 2 years (20% same age, 40% 1 year younger, and 40% 2 years younger). The reversals in 1992 were the opposite; older animals defeated younger ones that ranked higher (53% of reversals to older females) and 82% of these encounters involved individuals with 2 years of each other's age (21% same age, 40% 1 year older, 21% 2 years older, 18% 3 years and older). In addition, there were a few intransitive triads for both years of the study (1991: 6 of 391; 1992: 18 of 1017).

Another way to assess the stability of a dominance hierarchy is by comparing the outcomes of

repeated interactions between the same two goats. The proportion of dyads in which the winner changed between interactions was 17% over the 2 years (Table I), about the same as the proportion of interactions whose outcomes were opposite to that predicted by the rank of the interacting goats. The difference in mean age within dyads in which the outcome of successive interactions was the same and those in which the outcome differed was significant only when both years were combined (Table I). In 1992, of the 12 dyads in which the outcome of successive interactions differed, a single goat (number 86) was involved in five interactions and in all of these cases she was defeated by goats 3 years younger than her.

To test the stability of the hierarchy between years we compared the relative ranks of 20 females that were observed in both years by constructing two annual sub-hierarchies using only interactions between these 20 goats. Rank in one year explained about half of the variation in rank the following year ($r^2=0.51$, $P=0.0004$; Fig. 4).

When we tested for the best morphological correlate of dominance rank between individuals, we obtained conflicting results. The best cue was different between years. In 1991, horn length explained a greater proportion of the variance than other traits, whereas body mass was a good predictor in 1992 (Table II). There was a great disparity of coefficients of determination between

Age (years)	16	7	15	94	41	60	73	42	68	8	34	90	59	96	86	71	54	50	49	24	63	84	31	35	64	93	46	88	45	27
8	16	*	8				**			*	*	**	**	*	*	**	*	*	*	*	*	*	***	*	*	*	*	**	*	
9	7		*			*				*												*	*	*	*	*	*	*	*	
9	15	*		*			**			*	**	*	*	*	**	**	***	*	***	*	*	*	**	**	****	*	*	*	*	
6	94				*					*	*	**	**	**	**	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
10	41									*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	**	
8	60									**	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
7	73	*					*					***	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	**	
10	42				*	*						***	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	**	***	
4	68																*	*	*	*	*	*	*	*	*	*	*	**	**	
9	8					**	*			*	*	*	*	*	*	***	**	*	*	*	*	*	*	*	*	*	*	*	*	
10	34			*		*				*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
8	90	*		*		*	*	*	***	*	*	*	*	*	*	**	*	*	***	*	*	*	*	**	*	*	*	*	**	
6	59					*				*	*	*	*	*	*	*	*	*	*	*	*	*	**	*	*	*	*	*	**	
7	96							*	**	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	**	
6	86									**	*	*	*	*	*	*	*	*	*	*	*	*	***	*	*	*	*	*	**	***
7	71													***	**	*	*	*	*	*	*	*	**	**	*	*	*	*	*	
7	54		*											**	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
5	50																					*	*	*	*	*	*	*	*	
7	49																			**	*	*	*	***	*	*	*	*	***	
3	24																*	*	*	*	*	*	*	*	*	*	*	*	***	
6	63						*										*	*	*	*	*	*	*	*	*	*	*	*	*	
4	84																			**	*	*	*	*	*	*	*	*	*	
5	31																		**	*	*	*	*	*	*	*	*	*	*	
3	35																						*	*	*	*	*	*	*	
3	64													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	**	
3	93																						*	*	*	*	*	*	*	
4	46																						*	*	*	*	*	**	**	
5	88																						*	*	*	*	*	*	*	
3	45																						*	*	*	*	*	*	*	
3	27													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	

Figure 3. Win-loss matrix for adult female mountain goats, Caw Ridge, Alberta, 1992. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting: 44%. Number of interactions: 305.

years for certain traits, especially body mass and horn lengths (Table II). These results must be interpreted with caution because sample sizes for morphometric traits were small.

Other studies of female ungulates have shown that older individuals usually win interactions. Older females won 89% of interactions in red deer (Thouless & Guinness 1986) and 92% in bighorn sheep (Festa-Bianchet 1991). For mountain goats, age was correlated with dominance rank (Table

II), and 66% and 69% of interactions between goats of different ages were won by older animals in 1991 and 1992, respectively. We compared the number of interactions won by older individuals in the two studies mentioned above with our results and we found significant interspecific differences (deer-goat: $\chi^2=82.09$, $df=1$, $P<0.001$; sheep-goat: $\chi^2=57.81$, $df=1$, $P<0.001$).

Although some ungulate species defend their young from potential predators and conspecifics

Table I. Outcome of aggressive interactions between mountain goat dyads that were seen to interact at least twice at Caw Ridge, Alberta, in 1991 and 1992 (number of interactions are in parentheses)

Year	No. dyads	Outcome of interactions		Mean age difference in years within dyad (range)		
		Same winner	Different winner	Same winner	Different winner	P*
1991	27 (66)	22 (61)	5 (5)	2 (1-5)	1 (0-2)	0.08
1992	71 (180)	59 (167)	12 (13)	2.3 (0-7)	1.25 (0-3)	0.06
						0.02†

*Mann-Whitney test comparing mean age difference within dyads in which the winner of successive interactions was the same or different.

†Difference for both years combined.

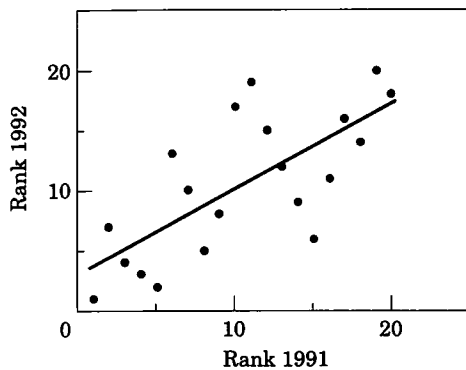


Figure 4. Relationship between dominance rank in 1991 and dominance rank in 1992 for adult female mountain goats.

(Berger 1978), goats in our study population do not appear to defend kids: we witnessed 27 incidents where kids were displaced by older goats, but the kids' mothers never retaliated or defended their young against harassment by conspecifics. Reproductive status (presence/absence of a kid) did not influence rank in either year (Table III).

In 98 h of focal sampling over a 2-year period, the dominance index of individual females did not influence the amount of time invested in different activities of the time budget (Kruskall-Wallis ANOVA: $P > 0.05$). The average (\pm SD) time that goats were active during the hour of sampling was

50.2 ± 10.9 min and 42.1 ± 12.2 min in 1991 and 1992, respectively. The difference between years was significant ($t = 2.184$, $df = 39$, $P = 0.035$). There was no relationship between dominance rank and foraging efficiency in either year (1991: $r^2 = 0.04$, $N = 19$, $P = 0.45$; 1992: $r^2 = 0.002$, $N = 24$, $P = 0.84$; Fig. 5). Furthermore, rank was not correlated with the percentage of time that goats were alert during focal observations (1991: $r^2 = 0.14$, $N = 19$, $P = 0.11$; 1992: $r^2 = 0.04$, $N = 24$, $P = 0.37$; Fig. 6).

DISCUSSION

Although the social system of mountain goats has been suggested to be based upon a dominance hierarchy (Chadwick 1977; Masteller & Bailey 1988), a detailed study of this system, with marked individuals, was lacking. Our results indicate that a dominance hierarchy does exist in our study population. Dominant individuals within dyads won the majority of interactions. Furthermore, this hierarchy is non-linear, indicating reversals of rank. Non-linear and non-random dominance hierarchies have also been found in other studies of female ungulates such as wild and captive bighorn ewes (Eccles & Shackleton 1986; Hass 1991), bison (Rutberg 1986), and feral cattle, *Bos taurus* (Hall 1986). Hass & Jenni (1991) found that for bighorn rams, the dominance hierarchy was

Table II. Regressions between dominance rank and individual characteristics of dominance status for adult female mountain goats in 1991 and 1992 at Caw Ridge, Alberta

	1991			1992		
	r^2	P	N	r^2	P	N
Age	0.44	0.001	21	0.62	0.0001	30
Weight	0.14	0.37	8	0.75	0.012	7
Horn length	0.84	0.0014	8	0.12	0.45	7

Table III. The effect of reproductive status on dominance rank in adult female mountain goats at Caw Ridge, Alberta, in 1991 and 1992

Reproductive status	1991			1992		
	Mean (\pm SD) rank	N	P^*	Mean (\pm SD) rank	N	P^*
Barren	12.15 ± 1.82	13	0.29	16.94 ± 2.01	18	0.28
Parturient	9.13 ± 1.93	8		13.33 ± 2.63	12	

* t -test for difference between mean ranks of barren and parturient adult females.

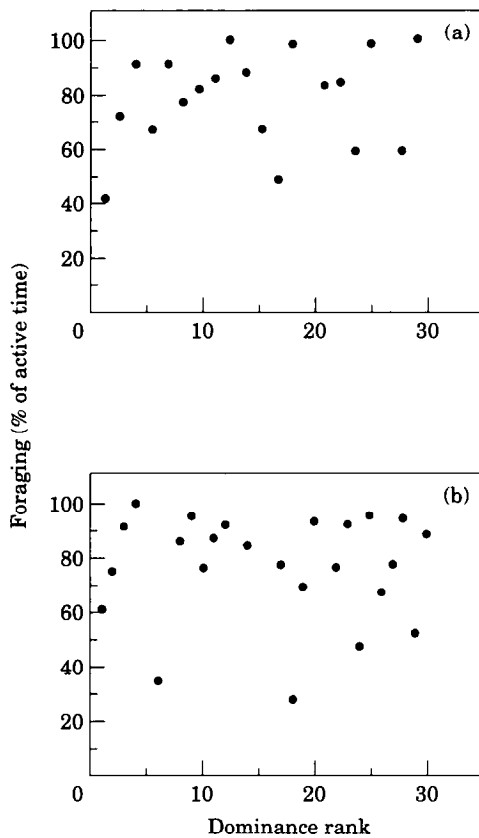


Figure 5. Relationship between dominance and foraging efficiency in (a) 1991 and (b) 1992 for adult female mountain goats.

linear and stable over many years. This suggests that a linear hierarchy is possible mainly when a contested resource (oestrous females) can be defended. It is not clear whether female mountain goats can defend a food resource, and this might account in part for the lack of linearity in their hierarchy. In summer, forage appears plentiful and widely distributed. In winter, however, it has been suggested that goats may defend foraging sites (Petocz 1973). In our population, goats commonly form large (≥ 15 individuals) groups during winter, so food defence, if it exists, is probably limited to the defence of snow craters (Barrette & Vandal 1986). Use of snow craters is itself very limited, because most winter foraging is done on grassland exposed by wind or snowslides (M. Urquhart, personal communication). As already stated, the lack of linearity is also influenced by the number of missing dyadic relationships.

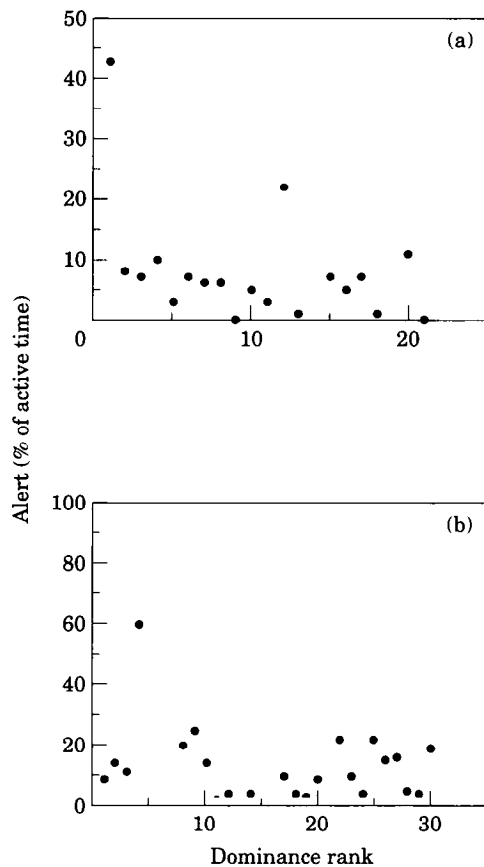


Figure 6. Relationship between dominance and percentage of active time spent in alert behaviour in (a) 1991 and (b) 1992 for adult female mountain goats.

Although this missing information would help us to better understand some of the relationships between adult females in the hierarchy, it is not clear whether individuals will interact with all other group members because it was our impression that some goats avoid the more aggressive females.

Among ungulates, dominance is correlated with age in female bison (Rutberg 1986), white-tailed deer, *Odocoileus virginianus* (Townsend & Bailey 1981), addax, *Addax nasomaculatus* (Reason & Laird 1988), red deer (Clutton-Brock et al. 1984; Thouless & Guinness 1986) and big-horn sheep (Festa-Bianchet 1991). Weight and age determined dominance in Appenine chamois, *Rupicapra pyrenaica* (Locati & Lovari 1991), whereas weight (Hirotsani 1990) but not antler size (Barrette & Vandal 1986) was correlated with

dominance in caribou. Rutberg (1983) suggested that young female bison learned to be subordinate from aggressive older cows. Thouless & Guinness (1986) followed the same argument as Rutberg (1983) suggesting that older hinds dominate younger ones when the latter are 1 or 2 years old and therefore considerably smaller in body size than older hinds, and that these relationships are maintained into adulthood, even when age differences in body size no longer exist. Festa-Bianchet (1991) suggested that the same may be true for bighorn ewes. These interpretations do not fully explain the social relationships of female mountain goats. Although most interactions were won by the older goat, interspecific comparison with red deer and bighorn sheep revealed that dominance rank was not as strongly correlated with age in mountain goats. Festa-Bianchet (1991) suggested that dominance was not worth fighting for in bighorn ewes because it did not give access to any major resource that could increase individual fitness. Similarly, Thouless & Guinness (1986) suggested that, for female grazers, dominant individuals do not seem to gain any benefit during foraging because most interactions do not involve replacement at a feeding site. Our results may imply that the benefits of aggressive behaviour for female mountain goats may be greater than for other female ungulates.

Another possibility is that during the ontogeny of behaviour, animals may possess a dominance rank in their respective age cohort and this may be possible if animals interact preferably with members of their own sex-age class (Rothstein & Griswold 1991). This could result in younger aggressive goats defeating older submissive females from another cohort.

The hierarchy of our study population was somewhat stable in time, as indicated by the correlation in rank between years. Hass (1991) also tested the stability of bighorn ewe hierarchies between years, and there were no statistical differences between her coefficients and ours (Hass: 1982–1983: $r=0.81$; 1983–1984: $r=0.78$; 1982–1984: $r=0.69$; goats: $r=0.71$). Thouless & Guinness (1986) suggested that red deer hinds have a stable hierarchy, but their measure was for dominance relations and not for hierarchies. Therefore we were unable to compare between-year stability of ranks for red deer and mountain goats. Although our results indicated a significant correlation of ranks between years, we suggest

that dominance hierarchies should not be considered stable when rank in one year leaves unexplained about half of the variance in rank the following year. Dominance relationships may be expected to remain stable between years to maintain a predictable social environment, thus reducing the risks of injury. Mountain goats may belong to a distinct society where the social climate is somewhat less stable than that found among other female ungulates.

Some studies have shown that dominant individuals have different time budgets than subordinates (Appleby 1980; Deutsch & Lee 1991). Dominant animals had priority of access to food in captive rhesus monkeys, *Macaca mulatta* (Deutsch & Lee 1991), red deer stags (Appleby 1980), woodland caribou (Barrett & Vandal 1986) and wintering mountain goats at a localized bait station (Masteller & Baily 1988). Although Geist (1974) proposed that the costs incurred in competing over food resources in female grazers likely outweigh possible benefits, Lovari & Rosto (1985) found that, in a group of Appenine chamois, dominance affected foraging efficiency. Prime-aged females had a greater number of bites per min and significantly fewer head-lifts per min, a measure of alertness, than did subadult females. These authors suggested that the reason why subordinates were alert more often than dominants was not predation pressure but the presence of potentially aggressive conspecifics (Lovari & Rosto 1985). Thouless (1990) suggested that, for red deer hinds, feeding competition is a passive process whereby subordinates avoid conflict with dominants by moving away from them during feeding bouts. He also found that dominant hinds had a better feeding efficiency than did subordinates (Thouless 1990). The data from Caw Ridge do not support this hypothesis for mountain goats. Dominant goats did not spend a greater proportion of their active time feeding when compared to subordinates.

According to Hamilton (1971) subordinate goats should be found more often on the periphery of the group and should therefore spend more time in alert behaviour. These results were found for pronghorns, *Antilocapra americana* (Lipetz & Bekoff 1982). Although predation is a major cause of death in this population (Festa-Bianchet et al. 1994), the goats often fed far (>400 m) from escape terrain and we found no difference between dominant and subordinate goats in the amount of

time they were alert. Alertness might have been due to both intraspecific aggression and risk of predation, and that might be the reason why there was no correlation between alertness and dominance. An investigation of how the risks of intraspecific aggression and predation affect alert behaviour in mountain goats should yield very interesting results, and may provide clues to why mountain goats demonstrate a higher level of aggression than most other female ungulates.

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