The effect of snow cover on the social behavior of bighorn rams and mountain goats

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The social behavior of bighorn rams (*Ovis canadensis canadensis*) and mountain goats (*Oreamnos americanus*) were studied quantitatively under different snow regimes in two winters. It was found that snow cover has little noticeable effect on the intensity of social behavior for mountain sheep during the rutting season. Thick snow cover reduces the total number of social behavior patterns per ram during the postrut; among mountain goats the number of social behavior patterns per individual remains consistently high. The thickness of the snow cover effects circumstantial changes in the function of specific behavior patterns among rams. Under extreme snow conditions, rams begin to exhibit rarely seen aggressive behavior. During deep snow, both species show an increase in overt aggressive behavior and a reduction in dominance displays. Under conditions of low snow and favorable weather rams increasingly engage in clashing, dominance displays, and appeasement behavior and reduce aggressive butting.

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Une analyse quantitative du comportement social de mouflons bighorn (*Ovis canadensis canadensis*) et de chèvres des montagnes (*Oreamnos americanus*), sous différentes conditions d'enneigement durant deux hivers, a révélé que l'épaisseur de la couche de neige a peu d'effet sur l'intensité du comportement social de ces animaux de montagne, durant le rut. Une couche de neige épaisse réduit cependant le nombre total de comportements sociaux par mouflon durant la période qui suit le rut; chez la chèvre des montagnes, le nombre de comportements sociaux par individu est toujours élevé. L'épaisseur de la couche de neige entraîne cependant des changements circonstanciels dans la fonction des comportements spécifiques, chez le mouflon. En effet, dans des conditions d'enneigement extrême, on observe des comportements d'aggressivité qui sont rares autrement. Si la couche de neige est profonde, les deux espèces montrent un comportement d'aggressivité accentué et une réduction des manifestations de dominance. Si l'enneigement est faible et la température favorable, on observe, chez les mouflons, une augmentation des rencontres à coups de corne, des manifestations de dominance et des comportements d'apaisement et une réduction des comportements aggressifs. [Traduit par le journal]

Introduction

Observations on the social behavior of ruminants in the wild have been restricted largely to analyses of the rules governing the operation of these societies and descriptive accounts of behavioral repertoires. Several authors have already demonstrated how snow cover can affect the distribution, movements, and feeding behavior of northern ungulates (see for example: Formozov 1946; Nasimovich 1955; caribou (*Rangifer*)—Pruitt 1959, 1960; and Henshaw 1968; moose (*Alces alces*)—Ritcey, unpublished[2]; Des Meules 1964; Telfer 1967; Peek 1970; Kelsall and Prescott 1971; deer (*Odocoileus*) and elk (*Cervus canadensis*)—Verme 1968; Mackie 1970; Knight 1970; Ozaga 1968; and Bouckout 1972; pronghorn (*Antilocapra americana*)—Bruns 1969; mountain sheep (*Ovis*) and goats (*Oreamnos americanus*)—Geist 1971); however, little or no mention was made of the relationship between social behavior and snow conditions. I have found that for bighorn rams (*Ovis canadensis canadensis*) there are considerable differences in the employment of behavior patterns during winter seasons of dissimilar snow regimes. My data for mountain goats (*Oreamnos americanus*) also indicate a positive relationship between behavior and snow cover.

This report represents part of a larger joint study centered on the winter behavior and ecology of mountain sheep and goats which is being prepared for publication in the near future.

Methods

The study was conducted on the Palliser Range in Banff National Park, Alberta, Canada, over an 18-month period between September 1968 and June 1970. Observa-

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tions were recorded on form sheets and on tape as seen through a Zeiss–Jena 80/500 binocular spotting scope. In all cases, the observer was situated at least 2500 ft from the animals.

Behavior patterns listed in this report are those described by Geist (1968) for mountain sheep and Geist (1965) for goats. In addition, I recorded "horn push" and "body push" as separate patterns to be described later. The sex–age classes of sheep are the same as those used by Geist (1968, 1971), as is the terminology.

The data in Tables 2 to 5 are expressed as relative percentage of the total behavior patterns recorded for all observation hours made during the day. The behavior patterns summed in Fig. 1 included only those cited in Tables 2 and 4 for sheep and goats respectively; however, additional data not recorded in Table 2 were used for sheep for the months of October through December. During weekly trips snow cover was measured on the slopes occupied by the animals.

Results

A. Sheep

Numerical Change in Behavior Patterns

In Table 1 is a summary of the snow depths for the two seasons taken when the social data were gathered. Figure 1 indicates the fluctuation in number of behavior patterns per individual per hour from the prerut through March for bighorn rams on the Palliser Range. Regardless of snow cover, frequency of social encounters during the prerut and rut remain constantly high. During the winter of 1968–1969, the number of patterns per individual dropped from 9.0 in December to 1.3 in January and remained below 1.0 through March. The comparable figures for 1969–1970 are 9.3, 4.4, and 5.8. In both winters, we witness a decrease in social behavior at the end of the rut (December–January), which is also the time when rams depart from ewe company. However, the frequency of social behavior among rams during the postrut is substantially higher during the mild winter of 1969–1970.

TABLE 1

Average snow depths recorded on the Palliser Range* during two winters

Mon.	1968–1969	1969–1970
Oct.	1.8	0.0
Nov.	2.7	1.9
Dec.	9.8	2.1
Jan.	23.8	6.2
Feb.	22.3	1.2
March	15.1	3.1

*Snow depths are expressed in inches averaged from readings taken on a weekly basis.

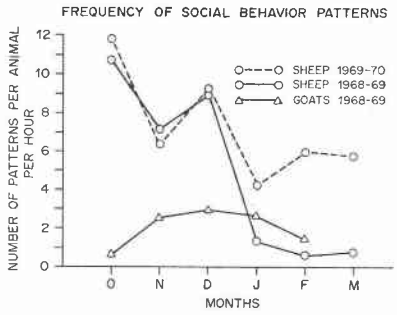

FIG. 1. Frequencies of social behavior patterns of bighorn rams and mountain goats during the winters of 1968–1969 and 1969–1970.

NOTE: Each point on the graph represents at least 4 days' observation, which in turn represents 8 h of continuous observation per day.

Storms that sometimes occurred in spring, depositing large quantities of snow in a very short time, had a pronounced effect on the incidence of social behavior among rams. During April, rams returned in large numbers from their distant ranges to a snow-free Palliser Range. Social activity is resurgent in spring and the new arrivals engaged in extensive group interactions and huddles. In 1969, a snowstorm dropped nearly 2 ft of snow on the mountainside in less than 36 h on April 29 and 30. On May 1, I watched continuously a group of 15 rams from 7.00 a.m. till 4.30 p.m. as they foraged in deep snow. Not only did they revert back to the typical midwinter activity pattern that I had seen earlier in the year (Petocz and Geist, in preparation), but social behavior was once again all but dropped from their routine. Only 37 patterns were performed during 6 h of activity which averaged to only 0.4 patterns per individual per hour. This is one example of several like incidents which occurred during the study and serves as a further illustration of the depressing effect of snow cover on the social behavior of rams.

Change in Type of Behavior Patterns

Just as snow cover appears to affect the frequency of social interactions, it also influences the type of behavior used by sheep. After the rut, social activity begins to diminish. Rams withdraw from ewe company at the end of December and form separate wintering bands on different geographic areas.

The figures listed in Table 2 represent observations of groups composed exclusively of rams. Probably the most obvious difference in social behavior between the two winters lies in the use

TABLE 2

Relative percentage of frequency of behavior patterns executed by bighorn rams on the Palliser wintering area

Time	Horn threat	Horn push	Body push	Clash	Butt	Contact	Front kick	Low stretch	Twist	Present	Lipcurl	No. patterns
Jan.												
1969	21.6	14.2	16.4	1.5	21.6	17.9	0	5.2	—	0	1.8	228
1970	6.4	0	0	6.4	19.2	23.2	8.0	26.4	4.0	5.6	0.8	125
Feb.												
1969	9.1	24.2	16.5	2.7	25.1	13.6	1.8	3.2	—	0.9	1.8	219
1970	1.2	0	0	7.9	17.6	12.1	20.7	21.3	9.5	6.4	3.3	329
March												
1969	9.5	4.8	0	4.8	19.0	40.1	9.5	4.8	—	4.8	2.4	168
1970	0.3	0	0	10.6	19.9	13.5	20.9	16.7	8.5	6.7	2.8	282

of behavior associated with unritualized combat. In the severe winter of 1969, almost all interactions occurred in feeding-area disputes. In this case, overt aggressive encounters were most common and collectively outnumbered all other behavior patterns. In addition, rarely seen aggressive patterns appeared in high frequency during 1969. These are as follows.

Horn push—Two or more rams feeding in a small area (snow crater or trench) often tried to displace a neighbor. In this case the dominant of the adjacent animals shoved his companion by leaning with his horns into the other's horns. The animals would push against each other with the side of the horns, one horn curl pressed against that of the other. The interaction rarely involved more than two animals. Dominant rams usually were successful in obtaining the contested position.

Body push—Like the former pattern, this behavior is also executed under crowded feeding conditions. The two antagonists, shoulder to shoulder, would attempt to dislodge one another by pushing with the broad side of their bodies. The interaction is initiated by the dominant ram who generally is successful in his attempt to dislodge the subordinate. Pushing with the body is a normal component of unritualized fights among rams (Geist 1969*a*, 1969*b*).

If we consider the horn threat, horn push, and body push as the major aggressive behavior, the following trend becomes apparent. In Table 3, the 1969 data show a much higher incidence of overt aggressive behavior than the 1970 data. Furthermore, during the severe winter of 1969, there is a decline in the frequency of overt aggressive behavior that coincides with overall snow depth (compare Tables 1 and 3); thick snow "stimulates" aggressive behavior. On the other hand, the amount of displays and ritualized interactions, such as the horn displays and clashing, decreased with snow depth.

Although butting was used in feeding-area disputes, it was excluded from the "agonistic" category since this was not its exclusive use. In 1969, butting was used more frequently to displace partners from feeding craters while in 1970 it was used in other social contexts. A butt was frequently delivered by a smaller to a larger ram just before horning or rubbing the face, horns, or body of the larger.

It was observed that the circumstances under which contact behavior, such as horning, licking, and rubbing, were used during the two winters were quite different. In 1969, such patterns were

TABLE 3

Relative percentage of frequency of overt aggressive behavior patterns typical of non-ritualized combat versus patterns typical of ritualized combat or courtship* for bighorn rams

Time	Overt aggressive behavior patterns typical of non-ritualized combat	Behavior patterns typical of ritualized combat or courtship
Jan.		
1969	52.2	8.5
1970	6.4	51.2
Feb.		
1969	49.8	10.4
1970	1.2	59.1
March		
1969	14.3	26.3
1970	0.3	66.2

*The first category includes the horn threat, horn push, and body push; the second includes the front kick, low stretch, twist, present, lipcurl, and clash. The figures represent a summation of the percentages of the various behavior as given in Table 2.

performed by subordinates generally *after* receiving agonistic behavior dealt out by dominants in competition for feeding spaces. The function here appears to be to appease dominant rams so as not to be chased away from the main feeding area. Successful appeasement became rare as snow depth increased. In 1970, however, when snow conditions were less severe, contact patterns were initiated by subordinate animals often without any prior engagement with a dominant individual, as happens normally in spring. In this case, such behavior did not appear to be issued for any immediate tangible gain.

The dichotomy in usage of contact behavior and butting prevents a numerical comparison of these behavior patterns between the 2 years. These examples nevertheless illustrate how snow cover can effect a shift in function of specific behavior pattern.

The above information clearly illustrates that while there occurs a gradual change in the frequency of mountain sheep social behavior through winter, snow cover exerts a considerable influence on both the magnitude and type of behavior patterns exercised by individuals. Thus, during the severe winter in 1969, rams executed agonistic behavior to compete for limited food resources and all but refrained from other social interactions. In 1970, on the other hand, food was much more accessible and intraspecific competition for this resource was almost nonexistent. Here mountain sheep interacted more extensively with ritualized patterns, their midwinter behavior being reminiscent of that which only began to occur in the spring of 1969. These data along with daily activity patterns and movements suggest that the ultimate reason for excluding social activity under conditions of high snow cover would be to conserve energy, while channelling necessary social efforts into procurement of forage. Furthermore, since such conditions elicited competition resulting in a high level of antagonism between individuals, any other types of social interactions would thereby be inhibited. It also appears that the observation of huddles (see Geist 1969*a*, 1971), displays, and clashing in midwinter indicates favorable forage conditions for rams, since such behavior is typical when the rams are in peak physical condition before the rutting season, or on lush pasture in late spring.

B. Goats

In comparison to sheep, mountain goats interact infrequently. Like sheep, goats are most active socially in the autumn and early winter (prerut and rut). At other times during the year the animals will generally segregate into "hierarchical" bands (Geist 1965; Holroyd 1967; De Bock 1970), and elicit little social encounter.

As the rutting season subsides, goat social activity declines. When social interactions do occur, they take on a hostile character; the expression and frequency of this hostility appears to depend on the depth of the snow cover. Although comparative data on social behavior are lacking between winters of 1968/1969 and 1969/1970, available data nevertheless suggest some trends in both frequency and nature of goat behavior from fall through midwinter.

Numerical Change in Behavior Patterns

Figure 1 shows the average number of patterns issued per individual goat per hour for each month from October through February 1968–1969. During the prerut and rut, the intensity of social behavior for both sheep and goats is high. However, during January and February the frequency of behavior remained fairly constant for goats, whereas there was an abrupt decrease in sheep social behavior after the rut in December (Fig. 1). Furthermore, the average number of patterns per individual was slightly higher for goats than for the more socially active sheep during the same winter of 1969. I account for this trend by the following reasoning.

January and February of 1969 were times of thick snow cover and considerable inclement weather. My observations agree with those of Geist (1965), Holroyd (1967), and De Bock (1970) that such conditions encourage goats to aggregate, thus reducing both the number of single animals and increasing the occurrence of mixed groups. With food accessibility limited by deep snow, interclass competition in bands rose, and dominant animals became very aggressive and antagonistic toward subordinates. This level of overt aggressive behavior was of commensurate frequency to the prerut and courtship behavior that occurred in November and December. Thus, while both sheep and goats displayed more aggressive behavior during January to February, 1969 (Tables 2 and 3; 4 and 5), the frequency of patterns per animal dropped

TABLE 4

Relative percentage of frequency of behavior patterns executed by mountain goats on the Palliser Range

	Agonistic behavior					Non-agonistic behavior								
Time	With-drawal	Rush and horn threat	Present threat	Horn jab	Butt	Low stretch	Horning	Sniff rear	Mount	Front kick	Flehmen	Wallow	Tongue flicker	No. behavior patterns
Oct. 1969	8.4	6.4	4.3	0.0	0.0	12.8	29.8	19.1	0.0	0.0	12.8	4.3	2.1	47
Nov. 1969	2.3	4.8	0.0	0.0	0.0	16.9	4.8	14.5	2.4	16.9	21.7	4.8	10.7	83
Dec. 1969	10.3	18.6	3.4	1.7	0.0	13.6	5.1	7.4	3.4	12.4	17.5	2.3	4.3	177
Jan. 1970	35.1	44.3	7.7	9.0	2.9	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	208
Feb. 1970	39.7	47.6	7.9	3.2	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	126

abruptly for sheep after the rut, while for goats there existed only a slight decrease (Fig. 1). In deep snow conditions, rams, in contrast to goats, will aggregate into cooperative feeding groups composed of individuals of similar dominance status. Here social encounters are rare and, although they sometimes occur, agonistic interactions are fewer than what we find in mixed goat groups. It can be predicted that comparative data from a mild winter with goats should show a numerical decrease in patterns after the rut, because in the absence of deep snow there would be little impetus for goats to form mixed groups with the subsequent aggressive interactions over feeding space.

Change in Kind of Behavior Patterns

Table 4 shows the categories of behavior recognized among goats during a 5-month period. Only one perhaps requires further clarification, as this was not described in earlier publications by Geist (1965) and De Bock (1970).

Withdrawal—This behavior is the most common response executed by a subordinate, in response to a rush, horn, or dominance display by an antagonist. Confronted by an agonistic dominant, a subordinate will often relinquish his position by turning from the aggressor with a hasty pivot on the hind legs, and running from the immediate vicinity. Frequently the ears are laid back, the tail is raised, and the animal defecates as it moves away.

A seasonal shift in employment of behavior patterns is apparent from Tables 4 and 5. The rush and horn threat, present threat, horn jab, and butt are all patterns which were executed in competition for feeding areas. These, together with withdrawal, a common response to the above patterns, I consider "agonistic" behavior and the remaining categories "non-agonistic" behavior. The relative percentages of each pattern falling in either of the above major categories have been listed in Table 5. The resultant trend now becomes clearer. In October, November, and December, non-agonistic behavior occurs in high frequency (prerut and rut). The reduction of agonistic behavior from October into November reflects a change from aggressive behavior (prerut), i.e., present threat, rush, and horn threat, to courtship behavior (see Table 4). In December the frequency of aggressive behavior begins to increase and coincides with the end of the rutting season, and the beginning of the deep-snow period of midwinter. From then on, i.e., January and February, agonistic behavior occurred to the complete exclusion of all other social encounters during competition for feeding craters.

TABLE 5

Relative percentage of frequency of agonistic versus non-agonistic behavior performed by mountain goats on the Palliser Range during 1969–1970*

Mon.	Agonistic behavior	Non-agonistic social behavior
October	19.1	80.9
November	7.3	92.7
December	34.0	66.0
January	99.0	1.0
February	100.0	0.0

*The figures represent a summation of the percentages of the patterns listed under the two classes in Table 4.

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