REPRODUCTIVE BEHAVIOR AND RELATED SOCIAL ORGANIZATION OF THE MUSKOX ON NUNIVAK ISLAND

A

THESIS

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REPRODUCTIVE BEHAVIOR AND RELATED SOCIAL

ORGANIZATION OF THE MUSKOX ON NUNIVAK ISLAND

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ABSTRACT

The sexual behavior and social organization of the muskox (Ovibos moschatus wardi Zimmerman) were studied on Nunivak Island, Alaska, in fall 1972 and summer and fall 1973.

Observation effort was concentrated on a single harem group for two months, during the height of courtship activity. Movements and fluctuations in the structure of this group are documented. There was no significant change in mean herd size as a result of the rut, suggesting the existence of a basic social unit independent of the influence of harem bulls. Harem bulls were in the 6-10 year age class. They exerted a stabilizing influence on the harem but did not direct its movements.

The rut extended from early July to mid-October. Copulation occurred on September 4 and 5. General patterns of sexual and agonistic behavior are described. Changes in activity patterns as a result of the rut are shown. Bulls displayed more marked changes than cows or juveniles. The proportion of time allocated to sexual and agonistic behavior increased at the expense of maintenance activity as the rut progressed.

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Most of all, I would like to thank Dr. John I. Johnson, one of

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TABLE OF CONTENTS

Table of Contents, continued.

Table of Contents, continued.

LIST OF TABLES

List of Figures, continued.

List of Figures, continued.

LIST OF FIGURES

INTRODUCTION

For sexually reproducing animals the behavioral selection process preceding the physical exchange of genetic materials at fertilization is one of the most powerful forces in evolution. Mate selection, which is a major function of courtship behavior, was the mechanism postulated by Darwin (1871) in The Descent of Man and Selection in Relation to Sex to explain the existence of the more extreme secondary sexual characteristics. Countless examples are available in nature of the broad range of morphologic and behavioral adaptations which evolution has produced solely to facilitate the process of fertilization. The fact that many of these traits seemed to run counter to the general pattern of natural selection by being detrimental for the survival of the individual prompted Darwin to propose a special theory to deal with sexual selection. As Darwin pointed out, when examining the evolutionary pressures which have led to the development of a species it is essential to consider the forces arising from within the group itself as well as those imposed by the physical environment.

Living in groups modifies and, in some respects, complicates the problem of determining which male will mate with which female. Gregarious animals have developed correspondingly complex social behavior to cope with this problem. For species such as the muskox, which have evolved polygamous breeding systems, determining which males will breed has extremely strong implications for gene frequencies

within the population and the long-term evolution of the species.

The work reported in this thesis was part of an overall study of the behavior and ecology of the white-faced muskox (Ovibos moschatus wardi Zimmerman) on Nunivak Island, Alaska. The major objectives of this portion of the study were to gain an understanding of the breeding behavior and social dynamics of the species which to this point have been very poorly understood. In order to meet these objectives, I sought to observe the behavior of free-living animals as they went through a complete cycle of courtship activity and to document the changes in relationships which occurred.

THE STUDY AREA

The Nunivak Island habitat presents a set of environmental conditions which are somewhat atypical of muskox range in other parts of the world. Tener (1965) states that this species is normally associated with an environment which has been termed a cold desert. The high arctic has very little precipitation, light snowfall and wide seasonal fluctuation in ambient temperature. Nunivak, in contrast, has a maritime climate with more abundant rain and snowfall and a temperature regime which is moderated by the influence of the Bering Sea.

The island is treeless, although willows up to eight feet high are found on a few restricted sites along stream beds. The dominant vegetation consists of grasses, sedges, and low shrubs. During the summer one is struck by the superabundance and lushness of the forage available to muskoxen. However, in winter most of this vegetation is locked under deep snow and ice. During the winter animals are restricted to the coastal dunes and escarpments where winds expose vegetation to grazing. The usable winter range constitutes only 1% of the total area of the island (Lent 1974). This situation leads to a dense concentration of muskoxen during the winter followed by wide dispersal in the spring. Bos (1967) has presented a detailed description of the plant communities, geology, and physical features of Nunivak Island,

and the reader is referred to this source for further information.

The island comprises an area of about 1700 square miles or 4403 km^2. The dimensions are 130 km in length by 97 km in width. It is located 30 km off the mainland between 166°00'W and 168°30'W longitude and latitudes 59°45'N and 60°30'N. The village of Mekoryuk on the northeastern end, with a population of 300, is the only permanent settlement.

The terrain is relatively flat with widely separated, low rolling hills. This factor plus the shortness of the vegetation permitted an observer to sight muskoxen at long range, particularly when he was located on a vantage point.

There are no physical barriers to muskox movements on Nunivak though much of the interior of the island is marshy and consequently receives little use.

The majority of behavioral observations were made on the western end of the island (Figure 1).

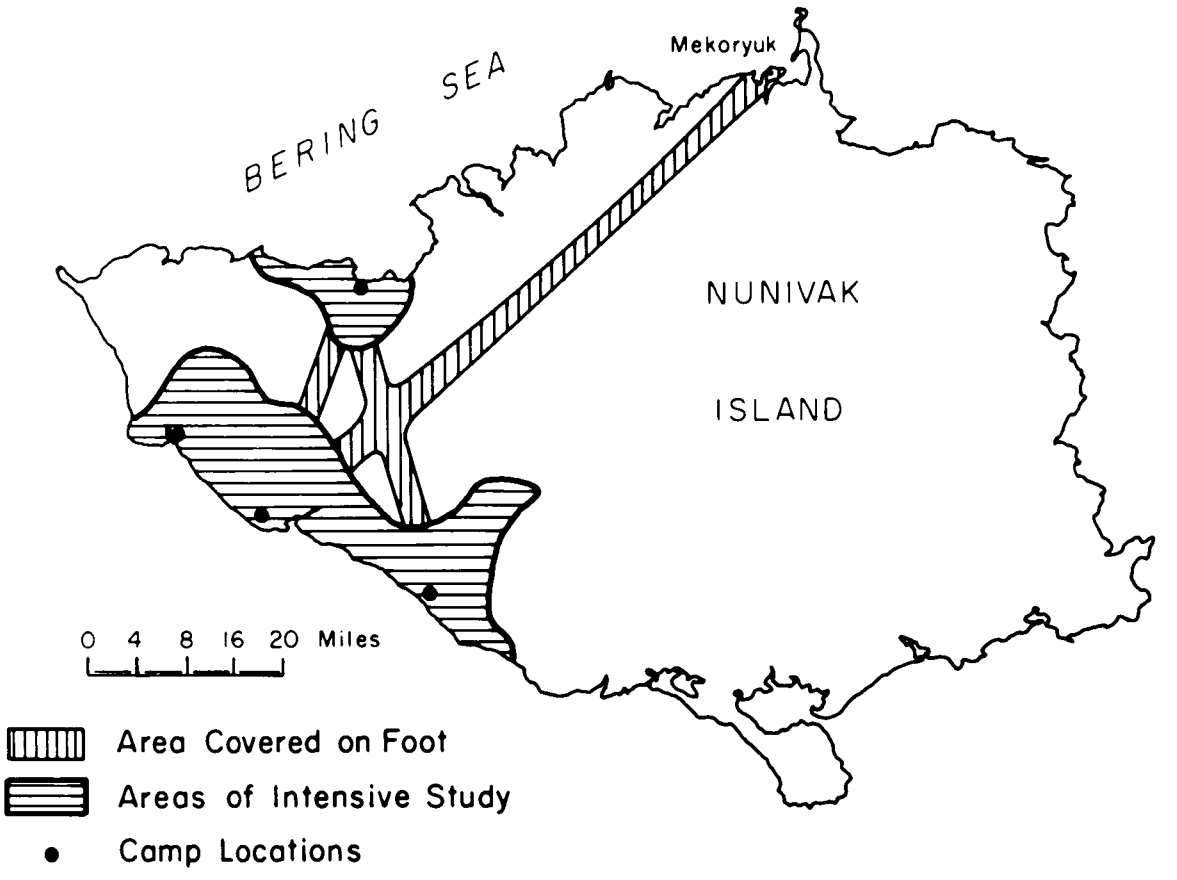


Figure 1. Map of Nunivak Island showing areas where observations were conducted.

THE STUDY POPULATION

The history of muskoxen on Nunivak began with the release of two bulls and two cows in the summer of 1935. All animals came from a group of 34 captured in East Greenland in 1931. After the first four muskoxen survived the winter in apparent good health the decision was made to transfer the remaining 27 animals to Nunivak in the summer of 1936. The introduction was successful and muskoxen quickly dispersed from the release site to occupy all parts of the island.

Bos (1967), Spencer and Lensink (1970) and Lent (1974) have compiled the available data documenting the rapid growth of the population following introduction. Muskox numbers reached a peak level of 750 animals in 1968 followed by a sharp decline during the spring of 1969. After this major die-off the population continued to decline and reached its lowest recent level in the spring of 1973 at 483.

During the period of the present study the population was estimated at 532 (summer of 1973) and appeared to be increasing.

Productivity of the Nunivak herd is among the highest recorded for the species. Table 1 summarizes existing data for calves as a percentage of the total population. Aside from a somewhat questionable observation by Urquhart (1973) the data from Nunivak and Devon Islands (Hubert 1974) show the largest proportion of calves yet reported. Urquhart's (1973) record is so unusually high that, if correct, it must reflect a

Table 1. Adult males and calves as percent of total population and percent males among adults for selected muskox populations.

Location	Year	Month of Survey	% adult oo of total pop.	% adult oo among adults including ♀♀ 4 yrs.+	% adult oo among adults including ♀♀ 3 yrs.+	% adult oo among adults including ♀♀ 2 yrs.+	% calves of total population	N	Source
Nunivak	1966	July	29.4	47.0	----	45.4	19.3	486	Refuge Rpt.
Nunivak	1967	July	----	----	----	----	18.4	651	Refuge Rpt.
Nunivak	1968	August	21.1	58.2	----	45.8	14.0	673	Refuge Rpt.
Nunivak	1970	early July	37.3	61.7	----	50.9	10.0	593	Refuge Rpt.
Nunivak	1971	mid-September	51.3	75.2	----	68.9	13.0	49;	Refuge Rpt.
Nunivak	1972	April	44.3	63.9	----	58.3	----	483	Refuge Rpt.
Nunivak	1973	March	38.8	62.0	----	52.1	----	530	Refuge Rpt.
Nunivak	1973	June-July	25.1	55.5	51.45	46.1	19.4	211	This study
Thelon Sanct.	1952	Summer	21.1	44.7	----	----	12.5	152	Tener, 1965
Foshein Pen.	1961	June	27.5	35.2	----	----	10.7	91	Tener, 1965
Inuo Haven	1958	Summer	36.0	50.8	----	----	6.6	86	Tener, 1965
Bathurst Isl.	1970	Summer	60.1	60.1	----	----	0	158	Gray, 1973
Bathurst Isl.	1971	Summer	55.2	55.2	----	----	0	232	Gray, 1973
Banks Isl.	1971	September	----	----	----	----	31.9	426	Urquhart, 1973
Melville Isl.	1972	--	----	----	----	----	10.5	466	Miller et al., 1973
Devon Isl.	1970	August	48.0	----	52.2	----	15.8	95	Hubert, 1974
Devon Isl.	1971	May	39.7	----	54.4	----	17.3	156	Hubert, 1974
Devon Isl.	1971	June	22.7	----	40.3	----	19.1	110	Hubert, 1974
Devon Isl.	1971	July	33.6	----	45.3	----	17.2	116	Hubert, 1974
Devon Isl.	1972	May	29.9	----	44.6	----	19.1	251	Hubert, 1974
Devon Isl.	1973	April	29.4	----	47.5	----	----	163	Hubert, 1974
Devon Isl.	1973	May	23.1	----	42.5	----	18.7	268	Hubert, 1974
Devon Isl.	1973	August	23.7	----	41.7	----	19.9	287	Hubert, 1974

population with a relatively large number of females. Unfortunately, no composition data is available to determine this.

In any case, a much more meaningful way of looking at productivity is to consider the number of calves relative to the number of reproductive age cows. Table 2 shows comparable data from the literature and the present study. Looking at the data in this way it can be seen that calving rates on Nunivak are much higher than anywhere else. This high rate of calf production can most probably be attributed to high levels of nutrition. Utermohle (in Lent 1974) has measured standing crop biomass on certain portions of Nunivak winter habitat, and found it to be significantly greater than on at least one other area of muskox range. Values he reported range from 2.32 kg/m^2 to 3.34 kg/m^2. The areas he sampled had been subjected to winter grazing by muskoxen. Hubert (1974) collected similar data on Devon Island and found values ranging from 0.176 kg/m^2 to 0.921 kg/m^2 on grazed winter range and from 0.275 kg/m^2 to 0.943 kg/m^2 on vegetation protected by enclosures.

Unfortunately there are no comparable quantitative data from other locations to determine how representative Hubert's data are of the total Canadian muskox range. Nevertheless, it is generally known that primary productivity in the high arctic is quite low.

That nutrition affects fecundity has been well documented in the literature on a wide range of ungulates. Factors which are primarily responsible for the high reproductive rate of the Nunivak population are that females frequently produce calves in successive years and breed at two years of age. It is generally assumed for high arctic populations

Table 2. Estimated calves per adult cow.

Location	Year	Month of Survey	Calves per female 3 yrs +	Calves per female 4 yrs +	Source
Thelon Game Sanctuary	1952	Summer	----	0.31	Tener 1965
Foshelm Peninsula	1951	June	----	0.29	" "
Lake Hazen	1958	Summer	----	0.17	" "
Devon Isl.	1970	August	0.46	----	Hubert 1974
Devon Isl.	1971	May	0.32	----	" "
Devon Isl.	1971	June	0.57	----	" "
Devon Isl.	1971	July	0.43	----	" "
Devon Isl.	1972	May	0.52	----	" "
Devon Isl.	1973	May	0.60	----	" "
Devon Isl.	1973	August	0.66	----	" "
Nunivak	1965	July-August	0.83	----	Bos 1967
Nunivak	1966	June-July-August	0.85	----	" "
Nunivak	1968	July	0.50	0.67	Refuge Report
Nunivak	1970	July	0.27	0.36	" "
Nunivak	1971	September	0.65	0.85	" "
Nunivak	1973	June-July	0.82	0.89	This study

that cows normally calve in alternate years (Tener 1965, Freeman 1970). In addition Tener (1965) reports that cows in the high arctic do not give birth until at least four years of age.

Thomson and Aitken (1959) have shown that poor nutrition does not delay the attainment of puberty in domestic sheep but that low levels of nutrition may alter fertility of ewes in their first estrus. Aleudal (1971a) documented the earliest ages of calving (two cows calving at two years of age) in wild muskoxen. These observations are from a small, introduced herd in the Dovre mountains of Norway. He attributed this early sexual maturity to the abundance of forage and the early onset of the growing season. Both of these factors are probably responsible for the relatively early breeding of females on Nunivak. There is evidence that few three-year-old cows produce viable calves during years with unusually harsh winter conditions (Lent 1974). This is in keeping with the findings presented above.

Calving in successive years can also be related to adult nutrition. Although calves were seen to nurse during the rut they grazed extensively. The short duration and infrequency of nursing bouts indicate that milk was a minor component of the calf's diet in late summer. Where forage was of low quality, however, calves might require larger amounts of milk to supplement their intake of plant material. Thus insufficient forage might not only tend to deplete the cow's condition directly but would necessitate higher milk production and enforce a longer period of dependency in her calf.

Baker (1964) has shown that when domestic cows are in poor

condition, nursing tends to inhibit the incidence of pregnancies. This would provide a mechanism which could give rise to calving in alternate years.

METHODS

The bulk of data presented here was collected in the field from June 6 to October 4, 1973. Two weeks were also spent on Nunivak in the fall of 1972, from August 24 to September 8, 1972. Additional information was gathered from observations of captive muskoxen at the Institute of Northern Agricultural Research farm at College, Alaska, during the breeding seasons of 1972 and 1973.

Classification of Muskoxen by Sex-Age Classes

Whenever muskoxen came under observation, an attempt was made to classify animals according to sex and age categories. It was possible to assign individuals to ten distinct classes as follows: calves, male yearlings, female yearlings, male two-year-olds, female two-year-olds, three year males, three year females, four year plus females, four year males, and five year plus males. Table 3 and figures 2-17 show the definitive characteristics of these categories.

Bulls older than 4 years were assigned a rank number from one to ten according to their estimated ages. Indicators such as the size of the space between the horn bases, weathering of the horn boss and general condition of the horns were used to determine age. Thus a class 1 bull would be approximately 5 years old. A class ten bull would be among the oldest encountered.

Table 3. Characteristics of various sex-age classes in muskoxen.

1. Calves: No evidence of horns; pelage short, curly; prominent white patch on forehead; sexes cannot be differentiated except by urination stance (Figure 2).
2. Yearlings: Slightly larger; straight guard hairs not covering legs; short horns extending out and forward; large white patch on forehead. (a) Males: horns thicker, more conical (Figures 3 and 5); (b) Females: horns flattened dorso-ventrally (Figures 4 and 6).
3. 2-Year-Olds: Body size of yearlings and 2-year-olds overlaps; rotund configuration; legs partly covered by guard hairs; prominent forehead patch. (a) Males: horns heavy, jutting forward (Figures 7 and 9); (b) Females: horns depressed slightly and upcurving, thin (Figures 8 and 10).
4. 3-Year-Olds: (a) Male: Body larger than female, smaller than mature bull; horns heavy, depressed and upcurving; horn base enlarged; small forehead patch; upper legs covered by guard hairs (Figures 11 and 13). (b) Females: body similar to mature cow; horn depression almost maximum; prominent forehead patch; upper legs covered by guard hairs (Figures 12 and 14).
5. 4-Year-Old Males: Nearly maximum body size; horn shape and tip to tip spread almost maximum; horn boss enlarged; gap between horn bases; forehead patch reduced (Figure 15).

Table 3, continued.

6. 4-Year-Plus Female: Maximum body size; forehead patch reduced; horn bases enlarged and exposed (Figure 16).

7. 5-Year-Plus Male: Maximum body size; horn boss very large, cracked; forehead patch almost forced out by horn base; small gap between horn bases, decreasing with age (Figure 17).

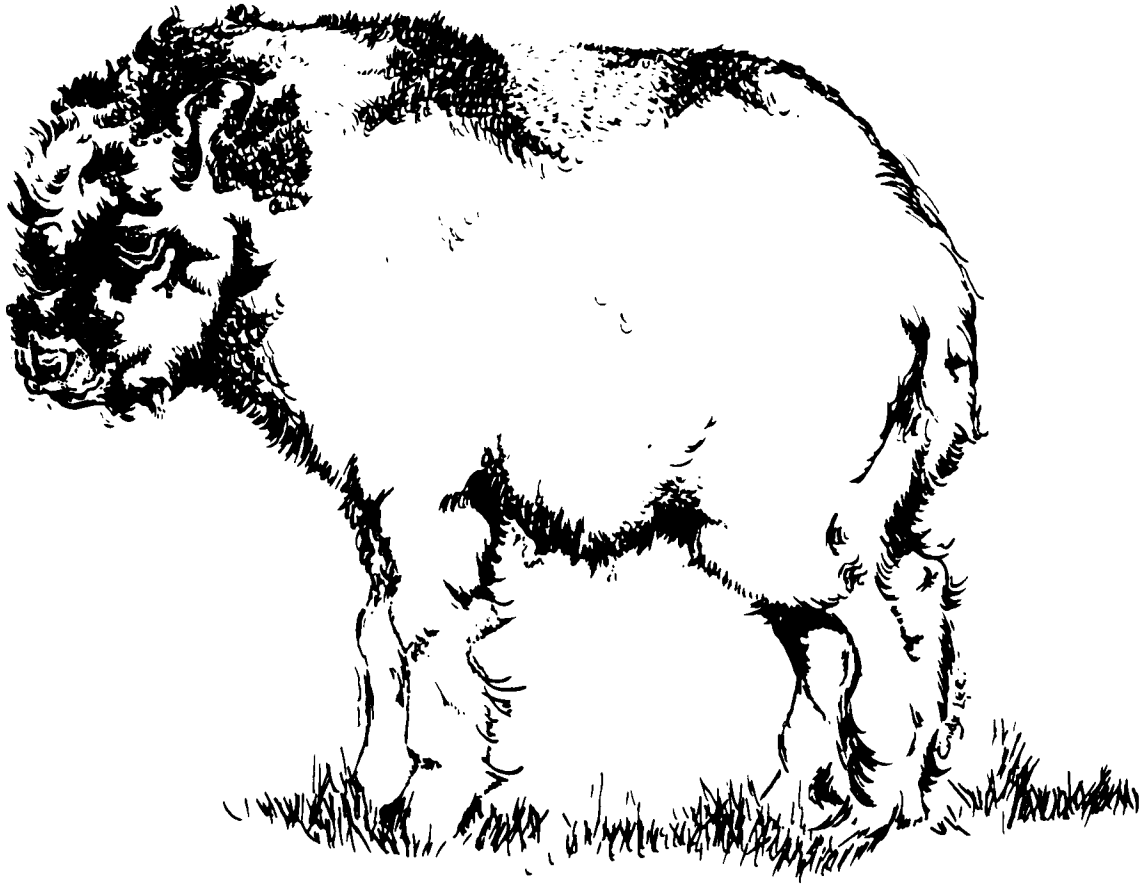


Figure 2. Calf.

Figure 3. Yearling male.

Figure 4. Yearling female.

Figure 5. Yearling male.

Figure 6. Yearling female.

Figure 7. Two-year-old male.

Figure 8. Two-year-old female.

Figure 9. Two-year-old male.

Figure 10. Two-year-old female.

Figure 11. Three-year-old male.

Figure 12. Three-year-old female.

Figure 13. Three-year-old male.

Figure 14. Three-year-old female.

Figure 15. Four-year-plus male.

Figure 16. Four-year-plus female.

Figure 17. Adult bull.

Identification of Individual Animals

In addition to being able to recognize sex and age classes it was considered essential to distinguish different groups and to identify individuals within a group for detailed analysis of social interations.

Although we were refused permission by the Alaska Department of Fish and Game to capture and mark animals it was still possible to identify groups and individuals with some certainty. Herds were identified by composition and the presence of one or more distinctive animals. When repeated contact was maintained with a group over a length of time, this method proved to be adequate.

Individuals within a herd were assigned an identification number whenever there was more than one member of a sex-age class within the group. Individual recognition was often possible using variations in characteristics such as color or horn shape. Underwool shedding patterns provided an excellent basis for recognition of certain individuals. The wool clings to the guard hairs on the neck and shoulders in large sheets as it is shed.

Facial features, particularly the amount of white on the face, could also be used to separate individuals. Several animals had broken horn tips or damaged bosses which provided an additional means of identification. When a fairly small group was observed over a period of several days, it was usually possible to recognize every individual with little difficulty.

Marking Efforts

In order to document the movements of lone bulls, a more positive identification system was required because these individuals were seen infrequently. Several methods were experimented with for applying water soluble fabric dye. Simply placing the dry powder in a plastic bag with a small quantity of water and throwing it at the animal proved most successful. The dye subsequently spread and was highly visible, particularly in the light hair on the back of the neck and hump. Five bulls were marked using this technique.

Observation Techniques

All observations were conducted on the ground in close proximity to the study animals. Whenever animals came under observation, I attempted to keep an uninterrupted record of activities for as long as possible. To maintain continuity, I made an effort to relocate a given herd on subsequent days. This proved to be quite successful once harem formation began and daily movements became more restricted. One group was repeatedly observed over a period of nearly two months at the latter part of the study period.

Continuous observation was maintained for as long as 14 hours by changing observers. It was rarely practical for one observer to remain with the animals for more than 8 hours at a time due to exposure to harsh weather conditions and the need to spend several hours walking from camp to the location of the herd. The second observer was kept informed of the movements of the group being observed by using citizens'

band "walkie-talkie" radios. Switching of observers was always done so as to minimize disturbance to the animals, usually during a period when all animals were resting.

The total time of systematic observation was 208 hours. Figures 18 and 19 show how this time was distributed both seasonally and diurnally.

By walking along ridges and hill tops each morning, it was usually possible to find the herd within a few miles of their location on the previous day. However, when weather or other factors caused a long delay between contacts, it sometimes became very difficult to relocate a group.

Data Recording

When observing a group I recorded the activities of all individuals. Time was noted at thirty-second intervals. The duration of certain behaviors was measured with a stopwatch. I kept a running account of the actions as they occurred, either by writing in field notebooks or by dictation into a Norelco pocket tape recorder.

Categories were developed to cover the behavioral repertoire of the muskox. A symbol was assigned to each behavioral category and entered into the field notes whenever that behavior was noted. The notes were then transferred to edge punch cards (E-Z Sort Systems Ltd.) and the cards were punched with the appropriate code. This system allowed me to extract all observations of any particular class of behavior. Information on the sex-age class of interactants in social

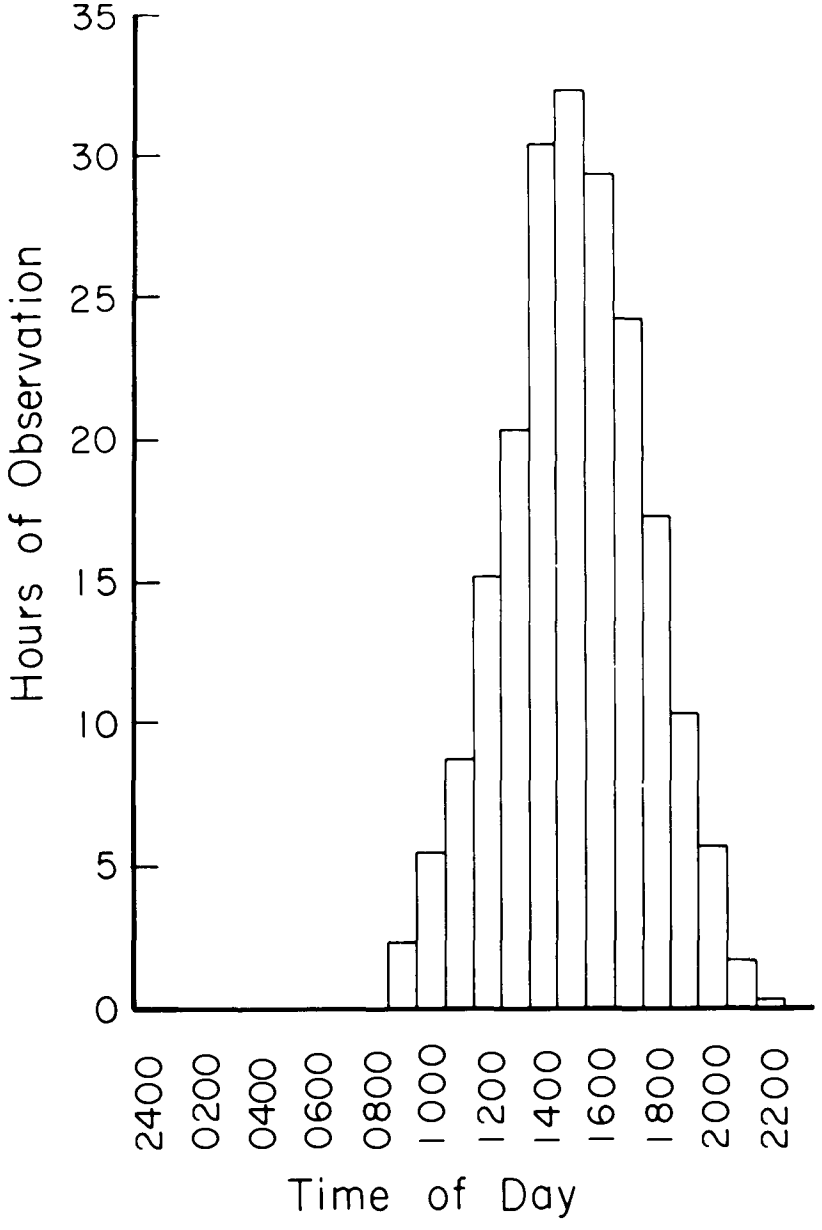


Figure 18. Distribution of observation time over a 24-hour day.

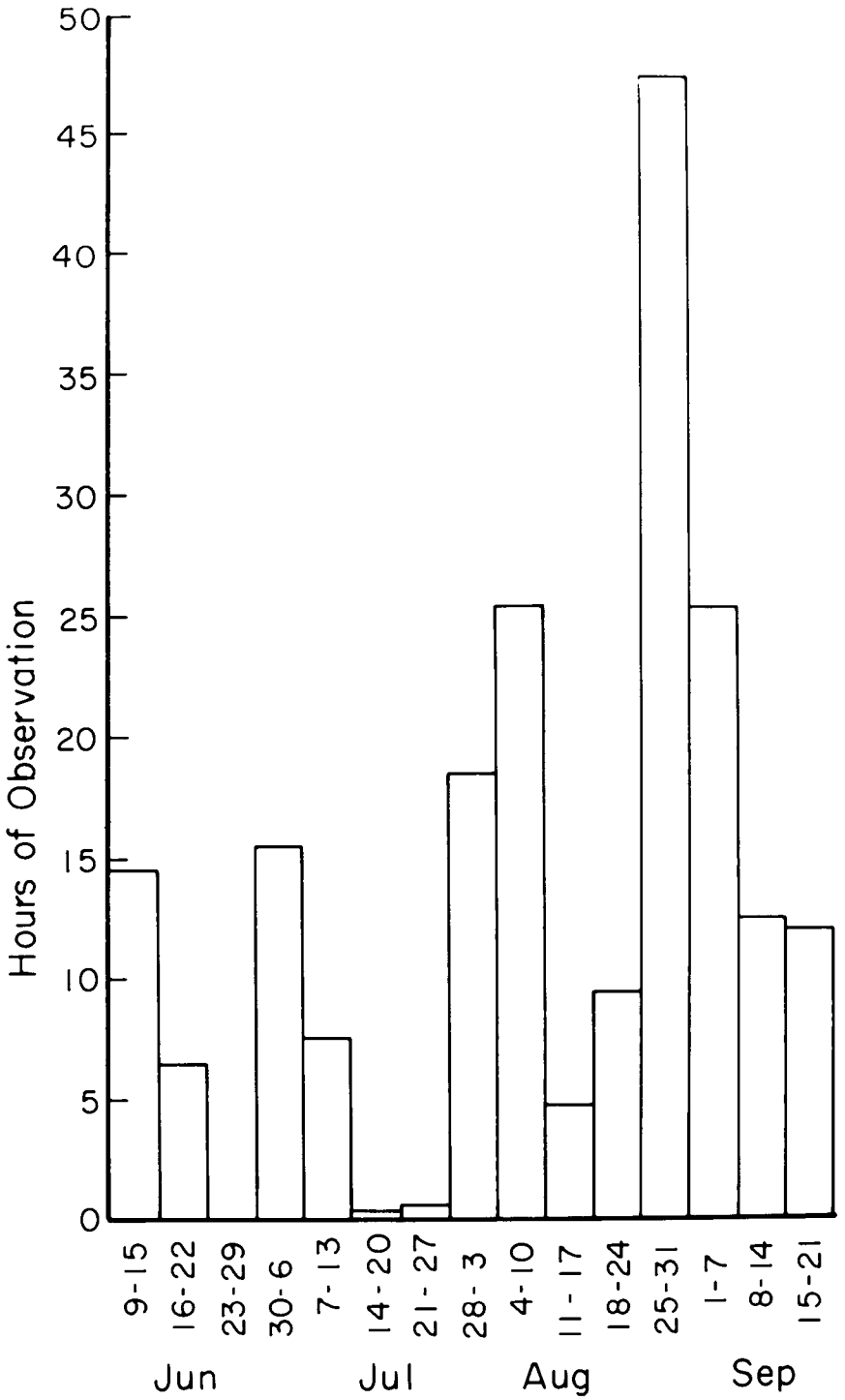


Figure 19. Distribution of observation time over the summer.

encounters was also entered on the cards, which permitted further selectivity in sorting data.

Whenever an animal was out of view or observations were stopped for any other reason, this was noted and the total time of observation for that animal was reduced accordingly.

Still and cine photography was used extensively to document behavioral sequences and for subsequent identification and aging of animals. Movie footage was particularly useful in supplementing written descriptions of behavior. Drawings were done from both still photographs and movie frames.

Muskox Response to Observers

Muskoxen are not particularly difficult to approach. The animals were most easily alarmed by seeing an upright human figure in motion. When observing animals a site was chosen which offered complete concealment if possible or at least reduced the apparent size of the observer. Muskoxen appear to have fairly acute eyesight and were especially aware of movement along the skyline.

Although the species seems not to be strongly oriented toward olfaction as a means of detecting enemies, a combination of both visual and olfactory stimuli was usually enough to disturb the group and alter their behavior. When the wind was unfavorable, the animals would frequently look toward my position which made it very difficult for me to move undetected. Where the terrain offered little concealment, one or more animals sometimes became aware of the observer's presence. The

herd's response to this situation varied. If the first animal were a calf or a yearling, adults generally ignored him and he quickly lost interest. If, however, I was observed by an adult, the entire herd would soon be looking in my direction. By remaining motionless while attention was focused on me or preferably, dropping completely out of sight, I soon became less remarkable and the group returned to their normal activities.

The observer to subject distance was generally 30 to 100 m for regular observations. Though it was usually possible to approach to as close as 5 m or less, extended observation at this distance was not possible and such close proximity was unduly harrowing for both subject and observer.

It was amply demonstrated throughout the study period that muskoxen do habituate to the presence of humans. Even after an extended period of contact on one particular day, they tended to be much more tolerant of movement and it became less important to remain fully concealed. The one group that was followed for nearly two months accepted human presence very well and only on rare occasions did they take fright.

RESULTS

The Rut

The rut of a species has been defined by Struhsaker (1967:31) as "the periodically recurring sexual arousal of that species." Fraser (1969:86) compares the commencement of the rut to a "dramatic puberty." However, as extreme as the behavioral changes associated with the rut are, levels of sexual activity rise and fall gradually so that it is not possible to establish rigid temporal bounds for the period of the rut in muskoxen. For the purposes of this paper, the rut was considered to begin with the first observations of courtship patterns and the formation of harem groups and end with the decline in sexual activity and the subsequent breakup of the harem structure. On Nunivak this period extended from early July to mid-October.

Sexual Behavior of Males

In this species courtship interactions are mainly the dominion of the male. Although endocrine cycles of females may ultimately determine the timing of insemination, the male is almost exclusively the driving force in the long sequence of events preceding copulation. His relationship to cow groups goes from extreme apathy or even aversion during the pre-rut period to unflagging almost constant courtship activity at the height of the rut.

During the pre-rut period bulls four years and older were more frequently seen as lone individuals or in pairs than as members of mixed sex herds. Of the pre-rut herds, 58 percent included no mature bulls while only 11 percent were without bulls during the rut. Data for 1965 and 1966 derived from Bos (1967) shows a similar trend with figures of 20 and 6 percent respectively.

Harem formation began early in July. On July 17, the first bull-cow interactions were seen. Those were not strictly courtship patterns but could more accurately be termed herding actions in which the bull controlled dispersal from the herd and began to assert his influence on group stability. Although the bull's behavior was similar to that shown later in sexual advances, the cows invariably reacted by running toward the group, apparently interpreting the approach as a threat.

By late July courtship patterns were being seen regularly. Bulls approached females as before to initiate courtship activities but at this time the cows were more likely to stand for the bull's attention. Now that cows were remaining stationary, the bull was able to perform more elaborate courtship sequences. The fact that only preliminary patterns were shown at this stage of the rut is interesting because it was my impression that the cow would have permitted mounting even though she were not in estrus. Cows were rarely seen to jump away from the bull as is the case in many other species. Geist (1971) reports that in mountain sheep the anestrous ewe attempts to interrupt courtship and rid herself of the ram. He also found that, like muskoxen, mature rams rarely attempted to mount an anestrous ewe. Walther (1968) and Krämer

(1969) saw similar male behavior in gazelles and chamois.

In the last weeks before cows came into estrus, the bull was active in almost continual testing of potential breeding females and even directed sexual interest toward yearlings and calves. The peak of rutting activity for one herd occurred during the first week of September somewhat later than has been reported by previous authors (Jensen 1904, Manniche 1910, Pederson 1931, Teuec 1954, 1965). At this time, over a period of a few days several copulations presumably with insemination were seen. Estrus in the six cows of that harem was very closely synchronized but since calving may occur anywhere from early April to late June this could not be true for the entire population. Intra-group synchronization of estrus has been reported for a number of other species (Fraser 1968).

Once cows had been mated the level of sexual activity shown by the bull declined rapidly. There is some difficulty in quantifying this change in that a few days after copulations were observed the harem bull was replaced by another and reduction in courtship activity may be merely a reflection of individual differences in bulls. There are measurable differences in the libidinal levels of males of other species (horse: Hafez et al. 1969c; domestic cattle: Hafez et al. 1969b; sheep, Hafez et al. 1969a). In fact the latter harem bull did seem to be less active than the former bull but since the first bull had also begun to reduce his level of sexual activity I considered it to be a general trend.

It would hypothetically be advantageous for the bull to remain with the harem even though all females had come into estrus and been mated,

so long as his energy expenditure was not too high, since there remains the possibility that a cow might not have conceived and would therefore enter a second estrus. Thus, testing should be expected to continue at a low level for some time and indeed this was the case. Evidence of the practicality of this strategy was seen on June 20, 1973 when a newborn calf was observed. Extrapolating back, using 35-36 weeks as the length of the gestation period (Alendal 1971b), results in an estimated conception date early in October.

Behavior Patterns

Behavior patterns involved in courtship by bull muskoxen have been described by Gray (1973). However, since he observed very little sexual activity in his study population most of the descriptions were based on few observations. Therefore, a more detailed account of observed courtship patterns is presented here.

Although there are no rigid distinctions between categories of behavior, the following ten components were most frequently displayed in heterosexual interaction and are therefore termed courtship patterns:

1. Orientation toward a cow

Before a bull approached a cow he shifted his orientation to face her in an alert posture with his head up and feet firmly planted. This posture was seen in other contexts, such as an aggressive orientation toward another bull or toward a human. The stare was directed with such fixity that the object of the bull's attention was usually quite apparent to the human observer.

2. The approach

As the bull moved from the orientation stance he dropped his head so that the muzzle was held low with the face perpendicular to the ground. He walked toward the cow with slow, deliberate steps, swinging the head from side to side as he moved but keeping his attention firmly focused on her. The pattern was identical in both sexual and agonistic advances, the most important component being his fixed concentration on the object of his approach.

Gray (1973:144) states that he was unable to determine that an approach was in progress until the bull had made contact with the cow. During the present study I found that I could usually anticipate an approach when the bull assumed the orientation stance. The directionality of the bull's stare gave an indication as to which cow was to be approached. Her reaction to the approach further confirmed my prediction. Whenever a cow saw the bull orienting toward her she became agitated and stopped feeding. As he moved toward her in the head-low approach she became increasingly agitated and often ran to meet him, thereby removing the threatening frontal aspect of the bull from her sight as quickly as possible. If she were resting she showed her apprehension by moving her head, wiggling the ears and sometimes rising to her feet.

3. Positioning

As the bull moves into contact with the cow, the pair take up one of a number of stereotyped orientations in relationship to one another. The bull and cow remain together for extended periods this way in close proximity, usually with a great deal of body contact. The amount of

contact in a particular position ranged from full length to none at all where the position was held with a slight separation between the animals.

Although there is a great deal of variability in positioning, all positions are variations of four basic patterns.

a. Bull-behind. The bull usually took up this position after approaching a cow from the rear. Most commonly the bull stood behind the cow with his body axis in line with hers. His head could either be in contact with her rump or some distance behind her. Initially he remained in the head-low posture with his horn bosses slightly below the level of her ano-genital region. From here he could raise the head to nose the vulva or perform any number of other courtship techniques. Frequently the bull stood behind the cow for some time, maintaining a constant space between them. As she moved ahead short distances, he waited for her to stop, then moved to his original position. Sometimes the bull moved up to stand with his body axis offset from hers resting the inside horn against her flank.

b. Parallel and Opposite. In this position, the cow and bull stood together with the axes parallel but reverse head orientation. Usually, they kept full lateral contact but sometimes remained a short distance apart. Frequently the bull stimulated the cow to move ahead by butting with his nose, hooking with a horn or performing a Laufschlag against her body. As she moved by him, he turned with her, sniffing the vulva as she passed.

c. Parallel. Body axes were again parallel but head orientation

was in the same direction. Few courtship patterns were performed from this position.

d. Perpendicular. This position was most variable. The only constant characteristic was that the body axes of the two performing animals were perpendicular.

Figure 20 is a symbolic representation of the permutations of these four positions which were observed in courting muskoxen.

e. Circling. Although the initial position was somewhat predictable on the basis of the direction of approach, the pair often moved into several different orientations during a single courtship bout. The cow usually remained stationary or moved only short distances when changing position. In moving around the cow the bull often maintained maximum body contact brushing against her with some force. The cow usually leaned toward the bull to counteract this pressure.

The behavior pattern which I have described here for muskoxen resembles an abbreviated tending bond or Hüten (Schloeth 1961), which has been reported for a number of gregarious ungulates. This bond occurs in domestic cattle (Schloeth 1961), caribou (Lent 1965), bison (McHugh 1958, Lott 1974) and mountain sheep (Geist 1971). In these species the tending bond probably developed as a response to heavy competition between males for the favors of estrous females. Since competing males are ever-present, a dominant male must remain in the vicinity of the female as long as she is receptive in order to prevent another bull from impregnating her. Because of the harem system, bull

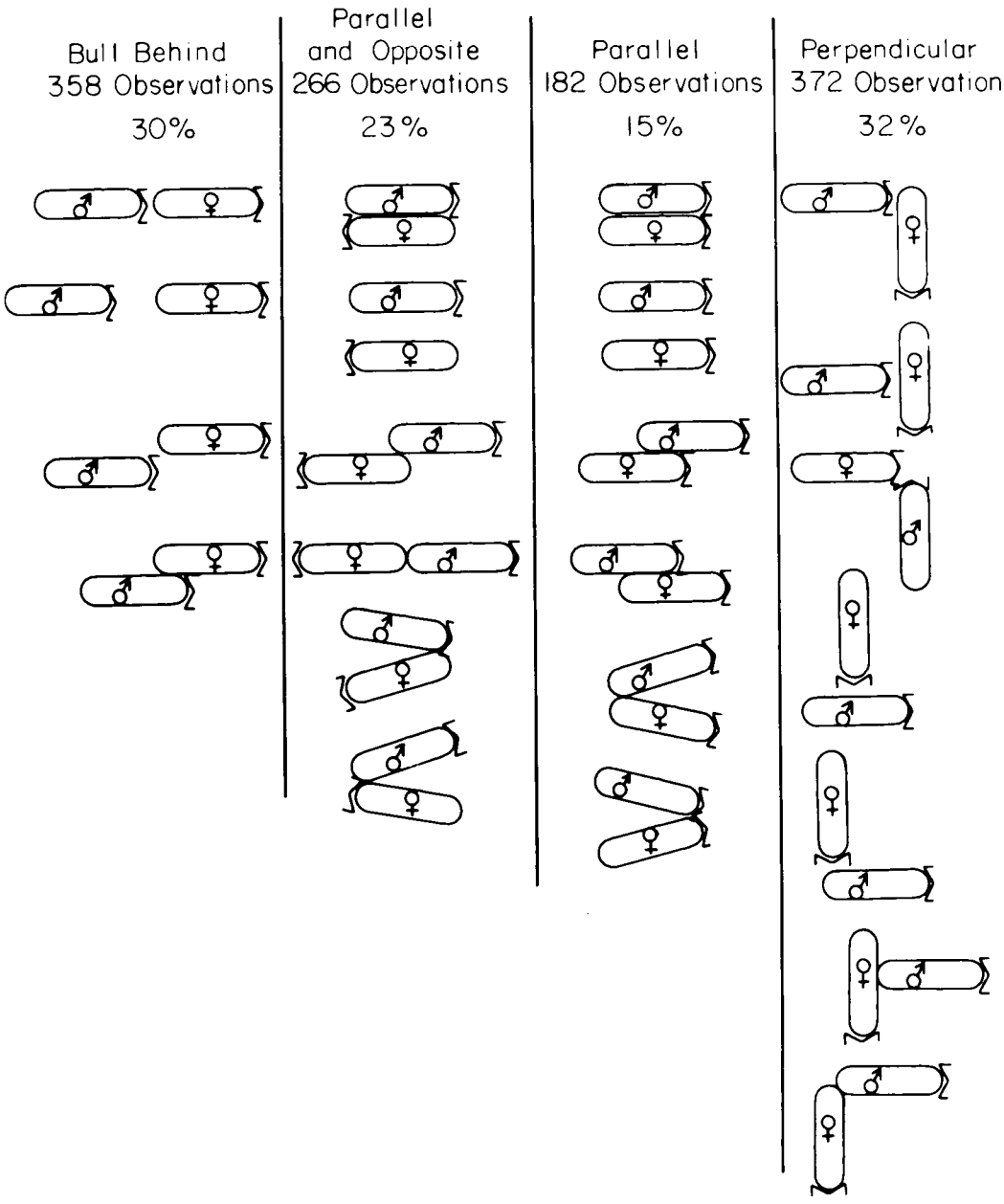


Figure 20. Variations in positioning.

muskoxen do not have to deal with constant competition for females. Therefore, if the tending bond is functional there must be another explanation for its existence. A very important result of this behavior may be to help suppress the female's inherent fear of the bull's approach and to prepare her for the intense fear-producing act of mounting and copulation. Gregarious animals must deal with two conflicting drives in their expression of herd behavior: the drive to associate with members of their own species and an opposing fear of close contact (Estes 1974a). Courtship necessarily violates the individual or social distance (Hediger 1961) within which an animal is highly vulnerable to attack by a conspecific. Courtship ritual develops to temporarily permit access by the male within the female's personal perimeter. Cow muskoxen are very much dominated by bulls and are visibly uneasy when approached by one. In this species a direct head-low approach is a high-level threat. The male's behavior in a sexual approach was indistinguishable from a threat directed toward another bull or toward a human observer. Positioning removes this frightening frontal aspect of the bull from the cow's sight. She runs to him rather than away, thereby removing the fright stimulus as quickly as possible. The cow seemed to favor the parallel and opposite orientation which is the antithesis of the head to head threat.

In addition to the removal of this visual threat, positioning places the bull within the individual distance of the cow and forces her to accept body contact and related potentially frightening movements which are a necessary part of courtship. As intensive courtship

Figure 21. Harem bull and cow in perpendicular position.

Figure 22. Bull performing head-twist as he circles the cow.

proceeds for several weeks prior to mating there is plenty of time for the cow to habituate to the close approach of the bull. This would tend to reduce the probability that she will run from him at the critical moment.

Schloeth (1961) has suggested that "guarding" in cattle is derived from the nursing orientation of the calf. This hypothesis also would seem to be a reasonable explanation for the origin of positioning in muskoxen. The parallel and opposite posture and the perpendicular position with the bull's head against the cow's flank are very similar to nursing stances. The bull was frequently seen to butt the cow's flank or inguinal region with his nose from these positions much as the calf butts while nursing. Mimicry of juvenile patterns by the bull may serve to reduce the cow's apprehension of the close approach by imitating a non-fear-producing situation, i.e., the approach of a calf. Gray (1973) also noted the similarity between some aspects of muskox courtship behavior and cow-calf relationships.

4. Head twist

Gray (1973) briefly described this pattern. It was displayed by the bull when in close contact with the cow. Most commonly it was done as the bull circled but could be executed from a stationary position or during the last part of an approach. In this display the bull started from the head-low posture but located the head toward the cow bringing the muzzle into contact with her body. His gait was stiff and exaggerated as he moved around her in the position (Figure 22). The

pattern strongly resembles the head tilt seen in agonistic displays but the orientation is toward the receiver rather than away. In addition the head-tilt is primarily a visual display but the head-twist is performed too close to the cow for it to have much visual significance.

5. Sniffing of rear

Olfactory investigation of the ano-genital region by the male is a common component of the courtship ritual of most mammals. In muskoxen the bull generally sniffs the cow's vulva soon after the approach and again several times during a courtship bout. The bull lifts his muzzle to the level of the ano-genital region either from behind or from the side (Figure 23). Often the bull butts or horns the cow, forcing her to move ahead from the parallel and opposite position so that he can inspect the perineum as she passes.

In other ungulates the male licks the perineal area during the sniff (sheep: Geist 1971; domestic cattle: Hafez et al. 1962b; mountain goat: Geist 1964; and elk: Struhsaker 1967). Because the guard hairs on the female's rump usually obscured the bull's muzzle it was not possible to determine whether licking occurred, although bulls sometimes performed tongue flicking movements after backing away from the cow.

Olfactory inspection of the vulva is presumably one of the methods the bull uses to determine the estrous state of the cow. The importance of olfactory clues was shown by Lindsay (1965) who compared the behavior of normal and anosmic sheep. Those which had their olfactory reception experimentally impaired courted estrous and anestrous ewes with equal

Figure 23. Bull nosing ano-genital region of yearling female.

Figure 24. Bull making Flehmen after nosing ano-genital region of yearling female.

frequency. Normal rams were able to discriminate in favor of estrous females.

Although the mechanism by which a male detects estrus in a female is poorly understood, the presence of the breakdown products of reproductive hormones in the urine of estrous females may be one clue (Fraser 1968). Since it is poor strategy for the bull to attempt to copulate with unreceptive cows, the ability to accurately determine the endocrine balance in her body before trying to mount would be highly advantageous.

6. The Flehmen

Bull muskoxen, like most male ungulates, perform Flehmen in response to certain olfactory stimuli (Figure 24). Upon receiving the releasing odor, particularly from the fresh urine of a female, the male goes into a stiff stereotypic posture with his head raised and the muzzle extended. The mouth is partially open and the upper lip everted. If the bull moves at all while caught up in the Flehmen it is only a few short steps. His total attention appears to be concentrated on the performance of the lipcurl and the stimulus which produced it.

Flehmen was displayed most frequently following ano-genital inspection of a cow but was also seen after the bull nosed the ground directly behind her. It is likely that in these cases he was reacting to the odor of urine or feces on the ground.

Mountain sheep (Geist 1971) and domestic sheep (Grubb and Jewell 1973) as well as many other female ungulates, urinate upon being

approached by the male. Geist (1971) has suggested that by urinating for the ram the ewe reduces the amount of harassment she must endure since she is able to escape from him while he is immobilized in the olfactory response. Cow muskoxen also urinate while being courted by the bull although the frequency of this response could not be accurately determined because of the long guard hairs on the cow's rump. Judging by the stance of the cow during ano-genital inspection it would appear that they urinate for the bull rather often. The reaction of the bull is a further indication that this was the case. In any event, the cow rarely made use of her opportunity to escape the bull even though he was incapable of following her for an average of 13 sec, the mean duration of the Flehmen. Nevertheless Flehmen still serves to reduce the levels of harrassment directed toward the cow in that it may allow a male to more effectively evaluate her receptivity.. The Flehmen response is apparently a mechanism for prolonging the retention of an odor by closing off the external nares and trapping it in contact with the nasal olfactory epithelium (Dagg and Taub 1970). Estes (1974b) has presented a convincing argument which suggests that the Flehmen serves to introduce odors into the vomeronasal organ. The major function of this organ, according to Estes (1974) is the detection of pheromones in the urine. Any behavior which would permit the bull to more accurately ascertain the reproductive status of the cow is advantageous to both partners in that it reduces unnecessary energy expenditure and enhances the probability that the timing of copulation will be correct. If the bull limits his courtship of anestrous females to preliminary

testing, then it is highly adaptive for the female to provide him with clues to indicate her condition. Since she can't really elude him if he is determined to court her, she will receive minimal harrassment by standing and permitting him to fully assess her physiological state through olfaction.

7. Laufschlag

The symbolic foreleg kick or Laufschlag (Walther 1958) occurs very commonly in the muskox courtship ritual. This kick is a generalized ungulate pattern found in giraffids and most bovids (Geist 1971).

When executing the kick the bull holds the foreleg stiff and straight, swinging it forward in an arc toward the receiver. The anterior surface of the hoof and lower leg strike the standing recipient on the side, flank, hip, between the hind legs or belly. If the animal is lying down the Laufschlag may be directed at the back or shoulders. It may also be performed in the air without contacting the animal to which it is directed.

There are conflicting opinions as to the derivation of this ritualized behavior pattern. Walther (1958, 1974) believes it to be a relic of primitive ungulate combat. A number of other opinions have recently been advanced to explain its origin in other species (Walther 1974), notably as a mounting intention movement in the lechwe (Lent 1969). For muskoxen, Walther's (1958) hypothesis still seems to be most applicable. The Laufschlag displayed by this species does not bear a strong resemblence to the mounting movement. In addition, the foreleg

kick appeared very regularly with other aggressive components such as nose butting and hooking with the horns when a bull attempted to compel a resting female to rise. In these instances the Laufschlag was more than symbolic. The force of the technique was such that I could hear the impact of the bull's hoof against the cow's spine or pelvis up to fifty m away. Several of these heavy blows were usually sufficient to cause the cow to stand for genital inspection. Thus a foreleg kick appears in two contexts: as a ritualized, relic behavior pattern and as a viable form of intraspecific aggression.

8. Chin-resting

Although this pattern is quite similar to chin-resting in domestic cattle (Hafez et al. 1969b, Swanney 1966) and in elk (Struhsaker 1967), there is seemingly greater variability in the behavior in muskoxen than in either cattle or elk. Chin-resting as I use it here is a lifting of the bull's head to rest the lower jaw anywhere on the cow's body (Figure 25). Chin-resting in cattle is apparently limited to the placing of the bull's chin on the cow's rump from behind. In muskoxen the chin was placed on the female's shoulder, hip or side as well as the rump and was performed from the parallel and opposite, perpendicular or bull-behind positions. The chin-rest is usually not held for an extended period. The bull simply lifts his muzzle to the dorsal surface of the cow's body and then lowers it again.

Chin-resting has been interpreted as a means of preparing the cow to accept the bull's weight prior to mounting and as another means for

Figure 25. Bull chin resting.

Figure 26. The rush.

the bull to determine the cow's receptivity. Non-estrous domestic cows avoid the bull but estrous females push back to counteract his force (Hafez et al. 1969b). This explanation also seems appropriate for the chin-resting pattern in muskoxen, even though there are minor differences in the execution of the behavior. Domestic cattle are usually bred under unnatural conditions and are not permitted an extended pre-ecital courtship period. For this reason behavior patterns may have been artificially abbreviated.

9. Rush

In this behavior the bull ran quickly at the cow from the bull-behind, in line position. He rose slightly on his hind legs and collided with some force against the cow's rear. As she stepped forward or was pushed by his momentum he slid the throat and chin backwards on the rump exerting pressure downward (Figure 26). No attempt was made to clasp the cow with the forelegs. Gray (1973) regarded the rush as being an incomplete mount which was foiled by the cow's refusal to stand. I believe it to be a completely separate behavior in which the bull has no intention of mounting, possibly a ritualized pattern derived from the mount. In many cases even though the cow stood and strongly resisted being carried forward the bull did not mount. The rush seems to be a logical intermediate step between chin-resting and mounting in which the cow is made to carry more of the bull's weight.

10. Mounting

By lifting the forward part of the body onto the cow's rump the bull brings the penis into contact with the cow's external genitalia. The mount must subsequently be maintained long enough to permit intromission and ejaculation. The mounting attempt was usually begun with the bull standing behind the cow, either directly in line or slightly off to the side. He often rested his head against her rump before mounting or remained a short distance behind her. He began the mount by charging forward, at the same time shifting his weight to the hind legs and lifting his chest onto her rump. In order to maintain his position, he must clasp the forelegs in front of the hip joints at the "fix point" (Hultnäs 1961). The bull moved his forelegs back and forth in a running motion in order to pull himself up high enough to make the clasp. The mounting posture is with the head down, nose held against the cow's back (Figure 27) similar to that of bison (McHugh 1958).

On several occasions bulls made unsuccessful mounting attempts from the side, rising up on the cow's back or shoulders before dropping back down.

Pelvic thrusting was rapid and performed rhythmically for up to ten seconds. The forelegs were continuously in motion along the cow's sides to maintain the position until ejaculation had occurred or the mount was interrupted.

The ultimate goal of male courtship is to achieve a mount with intromission and ejaculation. However, accomplishing a successful mount is apparently a rather difficult proposition for the muskox bull. Of

48 mounting attempts the clasp was maintained only 16 times even though the cow did not try to resist. Several physical factors would seem to be responsible for this difficulty. First, there is a great differential in weight between bull and cow. Furthermore, most of the weight of the bull is concentrated in the front half of his body, which must be supported by the cow. Many of the mounting attempts were unsuccessful simply because the cow was forced ahead under the bull's weight. Also, the anatomy of the bull with his deep chest and short legs is not well suited to clasping. These conditions make it extremely important that the cow does not resist the mounting attempt. The bull is not physically capable of forcing himself upon the cow and must have her cooperation in order to achieve intromission. Eliciting this cooperation is one of the primary objectives of the extended courtship period.

Vocalizations

As the bull approached a cow he frequently made a low, drawn-out roar. If she had been unaware of his approach, this vocalization usually caused her to notice it. The only other vocalization that I could detect associated with courtship was a short explosive snort through the nostrils which was done mostly at close range. This snort almost always preceded a rush, an attempted mount or any quick movement toward the cow such as the Laufschlag, nose butting or hooking with the horns.

Sexual behavior directed toward juveniles

Bulls regularly directed certain categories of courtship behavior toward animals which had not reached normal breeding age, specifically calves and yearlings. Courtship of juveniles was usually limited to genital investigation and preliminary courtship patterns. Mature bulls were never seen to mount a juvenile and might have caused injury to the younger animal had they done so. Yearling females were courted fairly often but yearling males only rarely. Bulls seldom directed courtship toward calves and no sexual preference could be determined.

Sexual behavior directed toward other males

Homosexual behavior among adult muskoxen is very rare. Unlike sheep, which treat all subordinate animals as females regardless of sex (Geist 1971), muskoxen definitely discriminate between the sexes.

Since all but yearling males were excluded from harems there were limited opportunities for homosexual behavior to occur. Two sequences were observed in which a harem bull directed courtship patterns toward a yearling male. Both of these occurred at the peak of the rut when courtship activity was at its highest level. The interactions were short in duration and included only investigation of the anal region and positioning. No sexual interaction was seen between adult bulls in all-male groups although observations of these groups were somewhat limited.

Sexual Behavior of Females

Response to Courtship by the Male

The role of the female in sexual exchanges is rather limited. The only thing that is required in order for a successful copulation to take place is that she stand as the bull mounts. There are three possible responses the female can make to the sexual advances of the bull. These are:

1. Submission

This is the most common course. As the bull approaches the cow, she stands for him or runs to stand beside him in the parallel and opposite position. She assumes a submissive posture with the head low and hind feet placed unusually far forward and apart. As the bull directs courtship patterns toward her, she may move in short series of three or four steps at a time but she does not try to escape from him. Often her movements are controlled by the bull who butts or horns her, causing her to move ahead.

2. Avoidance

Unreceptive cows sometimes attempted to escape by running or walking away from the bull as he approached. This response was most frequently seen in cases where the bull approached a cow which had strayed from the herd. As the bull approached from the direction of the group, the cow ran or walked in a wide circle around him back to the herd. When a cow sought to avoid the bull, she almost always ran to join the group. This strategy worked fairly well because the bull in moving after her would often begin courting another female and temporarily end

his pursuit of the first. Nonetheless, successful avoidance of the bull was for all practical purposes impossible since the cow always had to return to the herd. If the bull persisted in pursuing her, he would eventually succeed in his efforts. Cows which stood for the bull sometimes attempted to maintain the parallel and opposite orientation and thereby prohibit the bull from investigation of the vulva. This was usually not continued very long before the bull reacted aggressively toward the cow and she either permitted him to nose her ano-genital region or moved away from him. When a cow was approached while resting, she might attempt to avoid courtship by rolling onto her side and stoically accepting the foreleg kicks and butts he directed toward her.

3. Aggression

Instances where cows showed aggression toward bulls were extremely rare. The reasons for this are obvious when one considers the size differential between the bull and cow and the probable result of unrestrained combat. Female muskoxen do not pose a serious physical threat to the bull and in fact, would fare much worse if he were to respond to her aggression with a counterattack. Only two cases were seen where a cow acted aggressively toward a courting bull. In one of these, the cow kicked with the hind foot at a bull after he had pushed against her rear with his horn. This was unusual not only in that a female vented aggression on a male but she also used a defensive technique which had not been used by other muskoxen. The other instance was where a two-year-old cow met the bull's approach head on and engaged

him in a pushing match. The bull quickly broke it off and proceeded to court her in the normal fashion.

Behavior Patterns

Female courtship patterns are rather limited relative to those displayed by the bull. The following are descriptions of these patterns:

1. Alert posture

This posture was assumed by both bulls and cows when confronted with a distant stimulus which was perceived as potentially dangerous. In the context of courtship the alert posture was taken up in response to the orientation stare and subsequent approach by the bull. The head was up with the muzzle directed toward the bull. The nostrils were flared, and the hair on the hump appeared to be erected (Figure 37).

2. Positioning

Positioning was discussed in detail in the section on male sexual patterns. However, an additional comment on the female's movement during positioning is necessary here. When the bull and cow had remained stationary in one of the various positions for a time, the cow frequently moved away from the bull in a series of three or four quick steps and then stopped. The bull then moved up to her and often performed one of the more active courtship patterns such as chin-resting, Laufschlag, or rush. Geist (1971) has stated that receptive ewes run from a satiated ram thereby stimulating him to engage in further courtship activity. These symbolic escape intention movements seem to produce a similar response in bull muskoxen. This aspect of muskox courtship

is analogous to "pursuit type" courtship described for a number of species by Ewer (1968).

3. Face-rubbing

Several instances were recorded where a cow rubbed her face and horns against the bull's face or the side of his head. Mountain sheep rams frequently horn the faces of dominant rams (Geist 1971). The function of face horning in sheep is apparently to transfer secretions of the pre-orbital glands of one ram to the horns of another. Muskoxen also have a pair of well developed pre-orbital glands, which may serve a similar function in face-rubbing. Cows occasionally also rubbed the face against the bull's side or neck in a twisting motion, possibly depositing pre-orbital gland secretions on his body.

4. Body-rubbing

Highly receptive cows sometimes rubbed their bodies against the bull. This was done either by brushing the entire side back and forth against his side or by backing against him and rubbing with the rump.

Manifestation of estrus in females

Compared to many other ungulates, female muskoxen show very little overt expression of estrus or "heat." When in estrus, domestic cattle mount conspecifics regardless of sex and are in turn mounted by both cows and bulls (Hafez et al. 1969b). Female bison are often so aggressive in their courtship attempts that they interfere with the ability of the bull to mount by continually attempting to mount him (McHugh 1958). Estrous mountain sheep also actively court the male. Geist (1971)

reported observations of ewes attempting to elicit more active courtship from rams which were slow to respond.

Although cow muskoxen never displayed these levels of aggressiveness in courtship interactions, they did show certain behavioral manifestations of estrus. As cows approached estrus they began to orient toward the bull and took a definite interest in his courtship of other cows. In several cases an estrus cow forced herself between another cow and the bull. Instances were also seen where a cow moved to stand in front of the bull, then moved ahead in the short jerky steps which usually served to provoke a courtship bout from him. Face rubbing and body rubbing were further reflections of the high receptivity of estrous cows.

Copulation

Coitus in wild muskoxen has been witnessed by few people and only superficial reference to these observations have been given in the literature. Tener (1954, 1965) reportedly saw three successful matings but he failed to record the details of these occurrences. Alendal (1971b) briefly mentioned seeing a copulation between a young bull and a mature cow, once in the evening and again on the following day. Apparently there is very little information available concerning copulatory behavior even for domestic animals, although there are currently large numbers in captivity (Teal 1959, Wilkinson 1971). Gray (1973) relates two personal communications from persons who had observed coitus in domestic muskoxen but unfortunately, details are lacking.

During the present study I observed and photographed 16 copulations which took place on September 4 and 5. Pre-copulatory courtship in these bouts was not very different from that which had been observed in sequences which did not include copulation. The bull continually butted and nudged the cow ahead. She moved two to six steps and each time he followed. Then without any visible signal he mounted, rising up onto his hind legs, placing his chest on the cow's rump. He kept the forelegs in constant motion along the cow's sides in an attempt to remain mounted. The bull held his muzzle firmly pressed against the cow's withers for the duration of the mount (Figure 27). Because of the bull's shaggy coat it was not possible to see whether or not intromission had been achieved. I assumed that it had if the bull remained mounted for more than five seconds and performed pelvic thrusting. Thrusting began as soon as the bull achieved a stable mount. The average interval between thrusts was slightly under one second. Unfortunately it is not known whether they were performed after intromission or were merely an effort to locate the vagina. Dewsbury (1972) reports both types of thrusting patterns. In species which use pelvic thrusting only to locate the opening of the vagina there is usually a powerful final thrust which simultaneously inserts the penis and produces ejaculation. I saw no such final thrust in muskoxen copulations.

It is interesting to note that Flehmen was not seen in any of the courtship bouts where coitus occurred although olfactory stimulus should have been extremely powerful.

Before the mount, the cow stood in a submissive posture with the

Figure 27. Copulation.

head down and the muzzle pulled slightly back. The hind feet were apart and placed unusually far forward. There was no lordosis response. As she was mounted the cow was often forced ahead under the bull's weight. The bull walked on his hind legs as she moved in order to maintain his position and continued to thrust.

After the bull dismounted the cow remained stationary in the submissive posture for a time until his continued courtship caused her to move.

Repeat mounts occurred in rapid succession. Each copulatory sequence lasted from fifteen minutes to a half hour and included 5-6 apparently successful services. This number was remarkably constant regardless of the number of attempted mounts. For example, the bull (B1, see Figure 33) attempted to mount a mature cow 26 times in one 32-minute sequence. Of these 26 atrempts, 5 were successful. A two-year-old cow (2 yr F1) was mounted only 7 times in 16 minutes by the same bull but again 5 of these were completed.

Coitus lasted from 5 to 12 seconds with a mean of 7 and included an average of 6.5 pelvic thrusts.

While the bull was engaged in a coital sequence with a mature cow (F4) a younger cow (2 yr F2) attempted to interrupt courtship and solicit the bull's attention by pushing between them. He continued his courtship of the first cow but moved to the other when it was completed and copulated with her also. This was the most active courtship shown by a female and coincided with her coming into estrus.

Changes in Activity Patterns as a Result of the Rut

Figures 28 through 31 show the proportion of time allocated to specific categories of behavior broken down by weekly time periods over the months of July, August and September. Resting and consumptory behaviors are combined to give an indication of the energy allocated to maintenance. Sexual and agonistic behaviors together show relative energy expenditures which were directly attributable to reproduction. The first period (July 25-31), although not strictly part of the pre-rut, represents behavior which was largely unaffected by rutting activity. Looking at the data (Figures 28 through 31), it can be seen that bulls, cows and yearlings all spent more than 90 percent of their total time engaged in maintenance activities during that period. Calves allocated somewhat less time to maintenance (71.5 percent). This is probably due to the fact that they still nursed occasionally and thus needed less grazing time to meet their food requirements. In subsequent time periods, activities associated with the rut accounted for a much larger proportion of the total activity budget of adults. This was particularly evident with regard to the bull. Rutting behavior occupied nearly 30 to 55 percent of his time throughout the last 7 periods. In two of the time periods, the time allotted to courtship related behavior exceeded that of maintenance. From August 18 to September 7, there was a steady rise in the bull's rutting effort and a corresponding decrease in maintenance time. The increase in time allocation for rutting behavior by the bull is due to increased agonistic behavior which was highest during the September 1 to 7 period. This was the period when cows came into estrus and male competition was most intense. In these same three

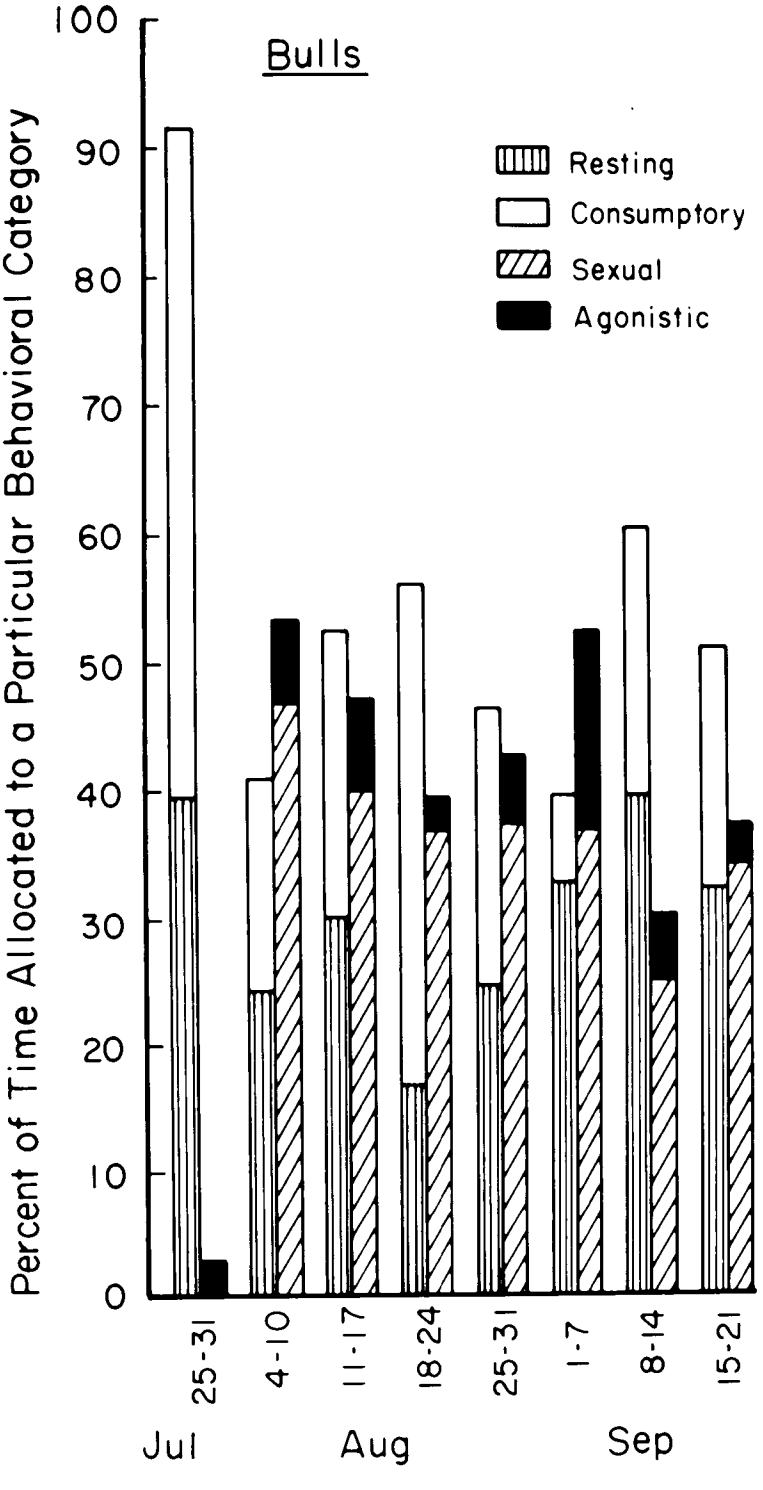


Figure 28. Seasonal changes in activity budgets among adult bulls: B1, B4.

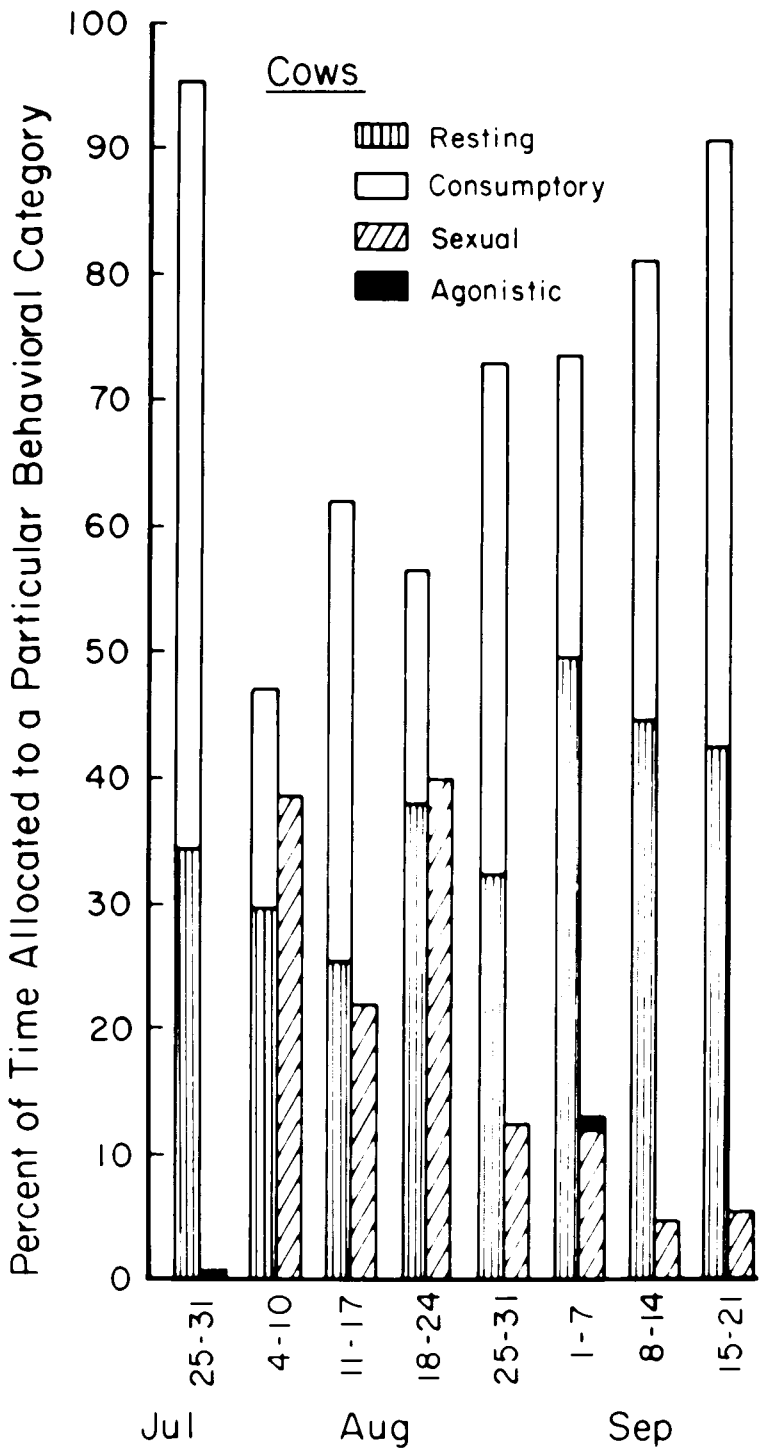


Figure 29. Seasonal changes in activity budgets among adult cows: F2, F3, F4, F5, F6.

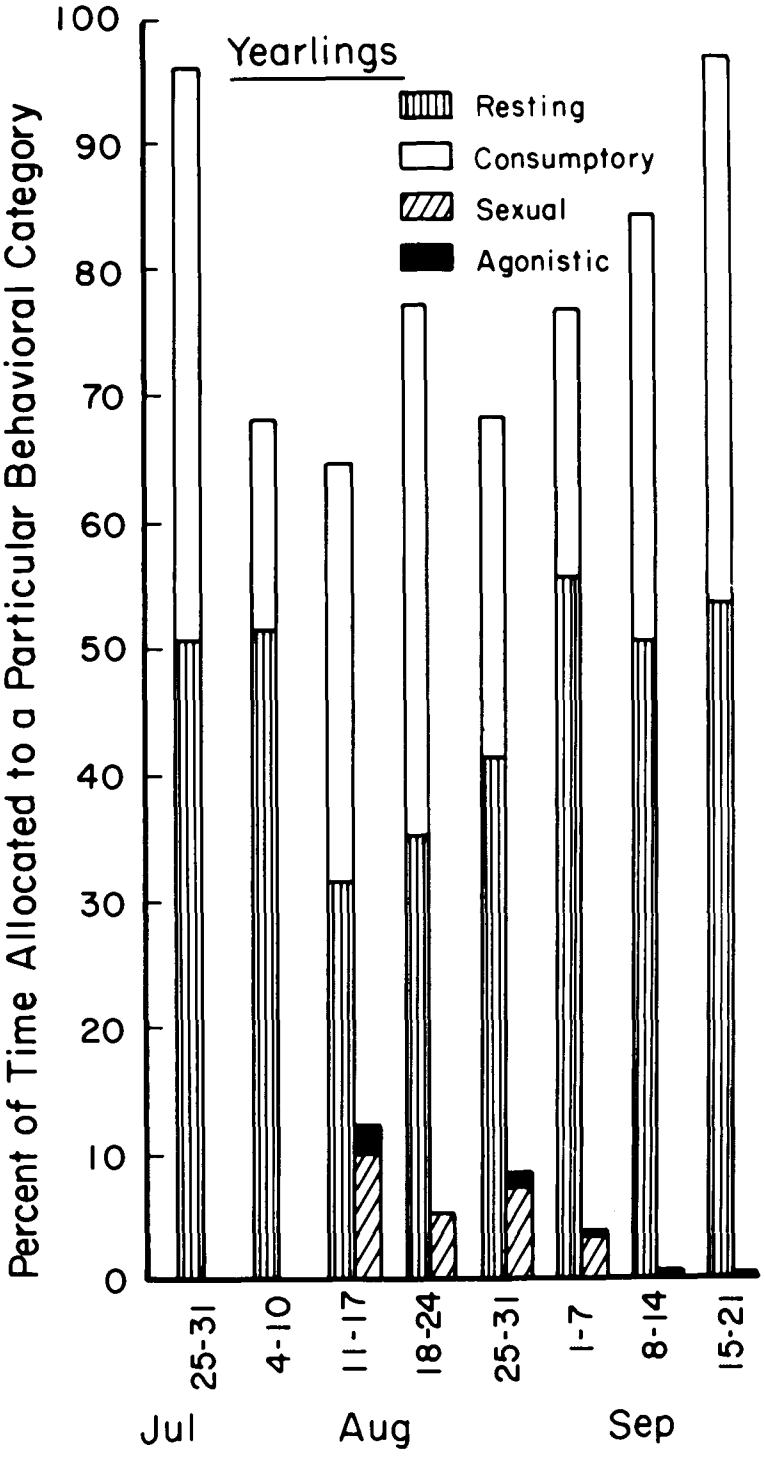


Figure 30. Seasonal changes in activity budgets among yearlings: ♂Y1, ♂Y2, ♀Y1, ♀Y2.

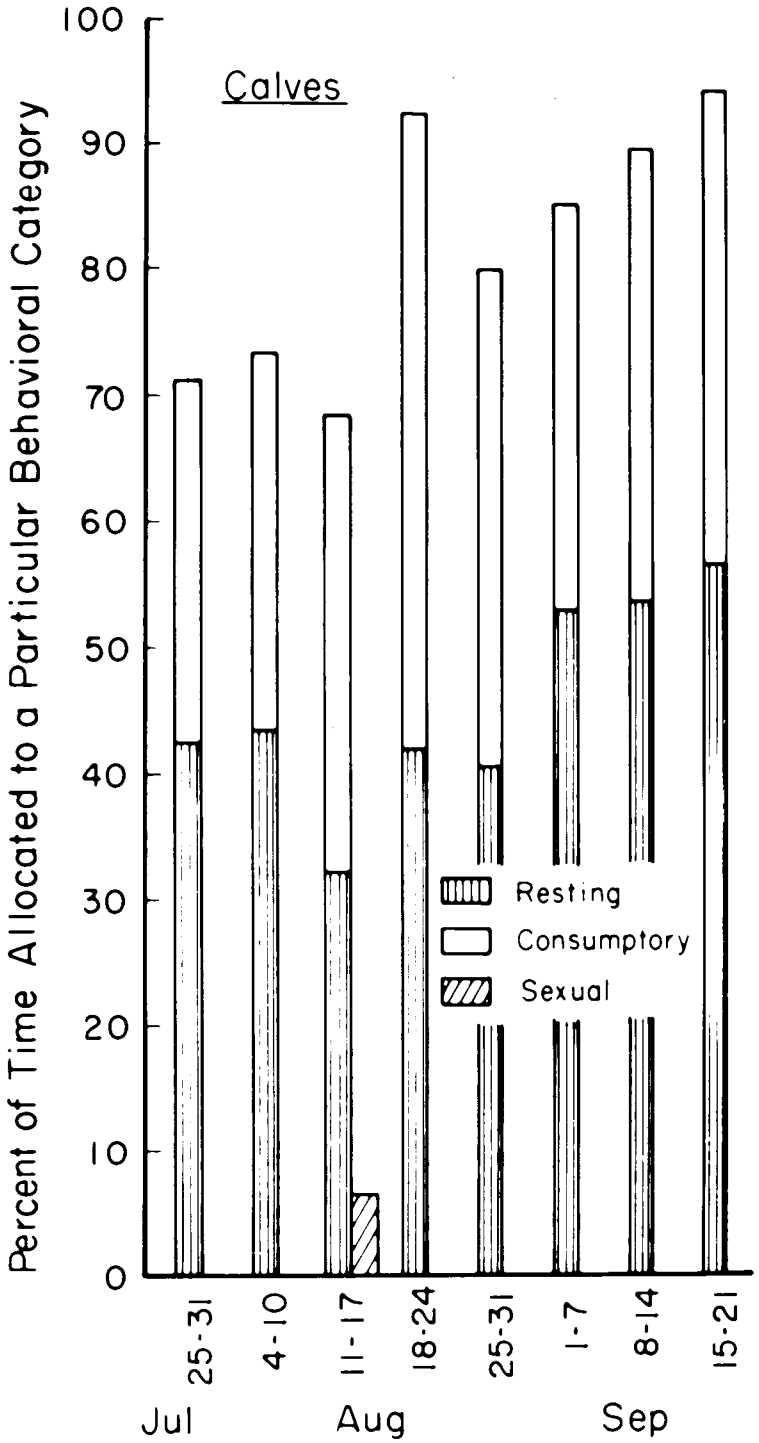


Figure 31. Seasonal changes in activity budgets among calves: C1, C2, C3, C4.

periods, the bull progressively increased the proportion of time spent resting. This was apparently related to the increasing demands imposed by intraspecific combat. The reduction in maintenance allocation was accomplished by a great reduction in grazing time. The substantial reductions in the bulls' grazing and rumination time throughout the rut can account for the weight losses reported by Hubert (1974) for rutting males in the Canadian Arctic.

Figure 29 for adult cows shows an initial large increase in courtship related behavior at the expense of maintenance in the second, third, and fourth time periods but a return, almost, to pre-rut levels in the last four. This was an effect of increasing harem size (Figure 33) which meant that the bull could devote less attention to each cow. Cows underwent weight losses during the first part of the rut in a population on Devon Island (Hubert 1974) though losses were not so extreme as those of bulls. Similar results would be expected from the information in figures 28 and 29.

Calves and yearlings (Figures 30 and 31) exhibited fairly minor alteration of activity patterns as a result of the rut when compared with adults. Data on yearlings were not separated according to sex because sexual differences in maintenance time allocation were small. However, females contributed 81 percent of the time allotted to sexual behavior.

Group Dynamics

Structure of Harems

A harem is a social unit which exists only during the rut in this polygynous species and is simply a temporary association between a single

bull and a group of cows. The bull maintains exclusive access to the cows in his harem by vigorously defending them against the approach of other males.

Although the initial formation of the harem is an unspectacular event it marks the beginning of a series of rather major changes in the daily activities of the animals involved. As is the case in elk (Altmann 1952), the prospective harem bull does not collect cows in forming his harem but merely joins an existing herd of cows, calves and juveniles and remains with them for the duration of the rut or until displaced by another bull.

Harem Size

The size of the harem is basically a function of the innate predisposition of muskoxen to aggregate rather than a reflection of the bull's ability to assemble a group around himself. If this drive were absent the efforts of the bull would not be sufficient to maintain the harem structure.

Table 4 shows the average herd sizes observed during the pre-rut and rutting periods. The pre-rut was June 1 to July 17; observations between July 18 and October 4 were considered part of the rut.

The averages are not affected significantly by changes in the number of bulls in the herd. Although pre-rut groups were more likely to contain no bulls, many of these groups included two or more. Herds seen during the rut very rarely had more than one bull. The average number of bulls observed by Bos (1967) was 1.75 in pre-rut groups and

Table 4. Average size of mixed-sex herds: pre-rut and rut.

Pre-rut	Number of Herds	Rut	Number of Herds	Source
9.65	20	7.39	33	Boe (1967) combined 1965-66 data
-----	--	7.81	47	U.S.F.W.S. August 1968 census data
8.28	25	8.23	29	Summer 1973 original data
-----	--	-----	--	
8.97	45	7.81	109	

1.03 in rutting herds. My own data showed even less effect: 1.31 bulls in pre-rut herds and 1.13 during the rut. These data fail to show a significant change in herd size with the onset of the rut, which would seem to suggest the existence of a basic social unit independent of the actions of the bull. Fuller (1960) has proposed that a similar unit occurs in the bison of Wood Buffalo National Park.

Like bison, muskoxen are by nature gregarious animals. This inclination is expressed particularly strongly in cows and juveniles. Cows seldom were seen alone and whenever circumstances caused them to become separated from the group they acted uneasy and quickly sought to rejoin the herd. It is this tendency to aggregate that gives rise to the social unit. Figure 32 shows the distribution of herd size data points for all four years. These data indicate that few mixed sex groups of less than 5 animals were seen. Small groups which were observed appeared to be transient and seldom existed as separate entities for long. The evidence suggests that animals in cow groups are most content when surrounded by several conspecifics, generally more than four. This fact tends to stabilize a group around the average harem size. If 5 of the animals in a group of 8 were to separate and move away together, the remaining three would soon seek to associate themselves with another group. Since the nearest herd in their vicinity would normally be the 5 that had just left, the likelihood of a recombination is high. Continuing on this theme it can easily be seen why large groups are so prone to fragmentation. A herd of 15 can split into two groups each meeting the minimum requirements of a basic social unit.

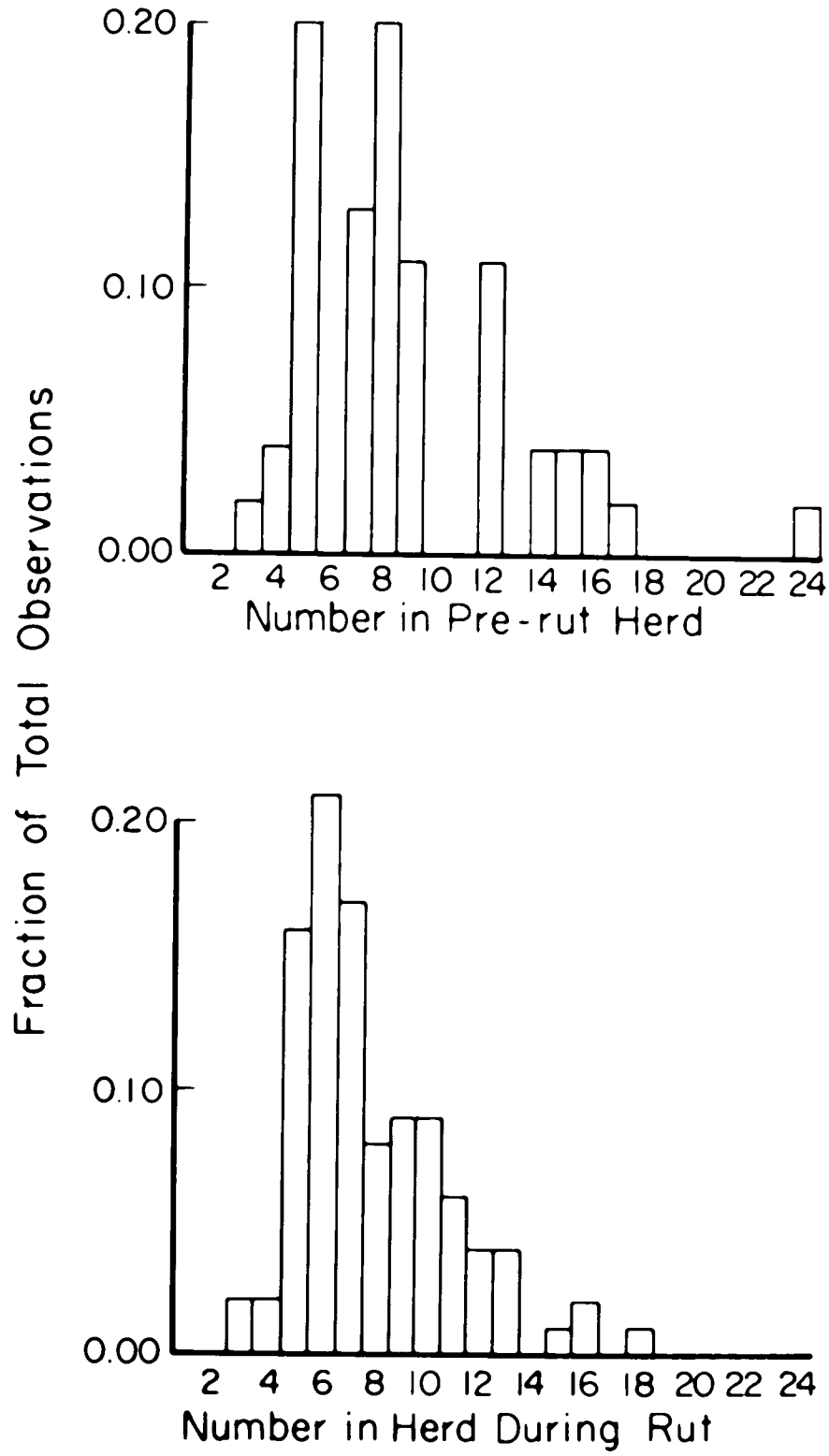


Figure 32. Distribution of herd size data points. Sources: Bos (1967) 1965 and 1966 data, U.S.F.W.S. 1968 census data, 1973 data this study.

Competition among males for cows appears to be a negligible factor in the regulation of harem size. Spencer and Lensink (1970) reported mean July herd sizes of 9.0 and 8.1 respectively in the years 1962 and 1964. These figures are comparable to the more recent data in table 4, even though the percentage of mature bulls in the population has increased substantially since then.

Age of the Harem Bull

Because the number of harems is small relative to the number of sexually active males, the harem bull is a member of a rather elite group. Bulls which are able to successfully acquire and defend a harem are active, aggressive animals in prime physical condition. Although bulls are capable of producing viable sperm by age 2 (Teal 1959, Tener 1965) under natural conditions few if any two-year-old males breed. On Nelson Island, muskoxen introduced as yearlings produced calves in the second year following release. Thus bulls must have bred at 2 years of age (U. S. Department of Interior 1975). Nevertheless, under more normal circumstances, inter-male competition restricts breeding to older bulls.

Table 5 shows the relative ages of bulls seen in the Nunivak population, both with and without harems. Ages given are according to an index from 1 to 10 based on qualitative comparison of such indicators as horn boss development, horn wear, and behavior. In terms of years, a class 1 bull is about 5 years of age and a class 10 bull is the maximum age reached by muskoxen (>20 years, Buckley et al. 1954). The approximate ages of 14 skulls ranked according to this method were compared to

Table 5. Relative ages of bulls observed during the rut: July 17 to October 4, 1973.

Designation	Age Class*	Observed in Harem	Observed in Lone or All-Male Group
M1	1-2		X
M2	1		X
M3	3	X	
M4	9-10		X
M5	8-10		X
M6	6-7		X
B1	2-3	X	X
B2	4-5	X	X
B4	2-3	X	
M7	2-3		X
M8	6		X
M9	2		X
M10	5-6		X
M11	6	X	
M12	4	X	
M13	2-3		X
M14	2-3	X	
M15	2-3	X	X
M16	1-2	X	
M17	10		X

*Not years; see text for explanation.

known ages obtained by analysis of cementum layers in incisor I (Lent 1974). The results indicated that observer judgments were acceptably close to the actual ages of the animals.

Looking at the data in table 5 it can be seen that harem bulls tend to be in the 6 to 10 year range. This is consistent with Hubert's (1974) assumption that bulls do not breed until 6 years or older in the wild.

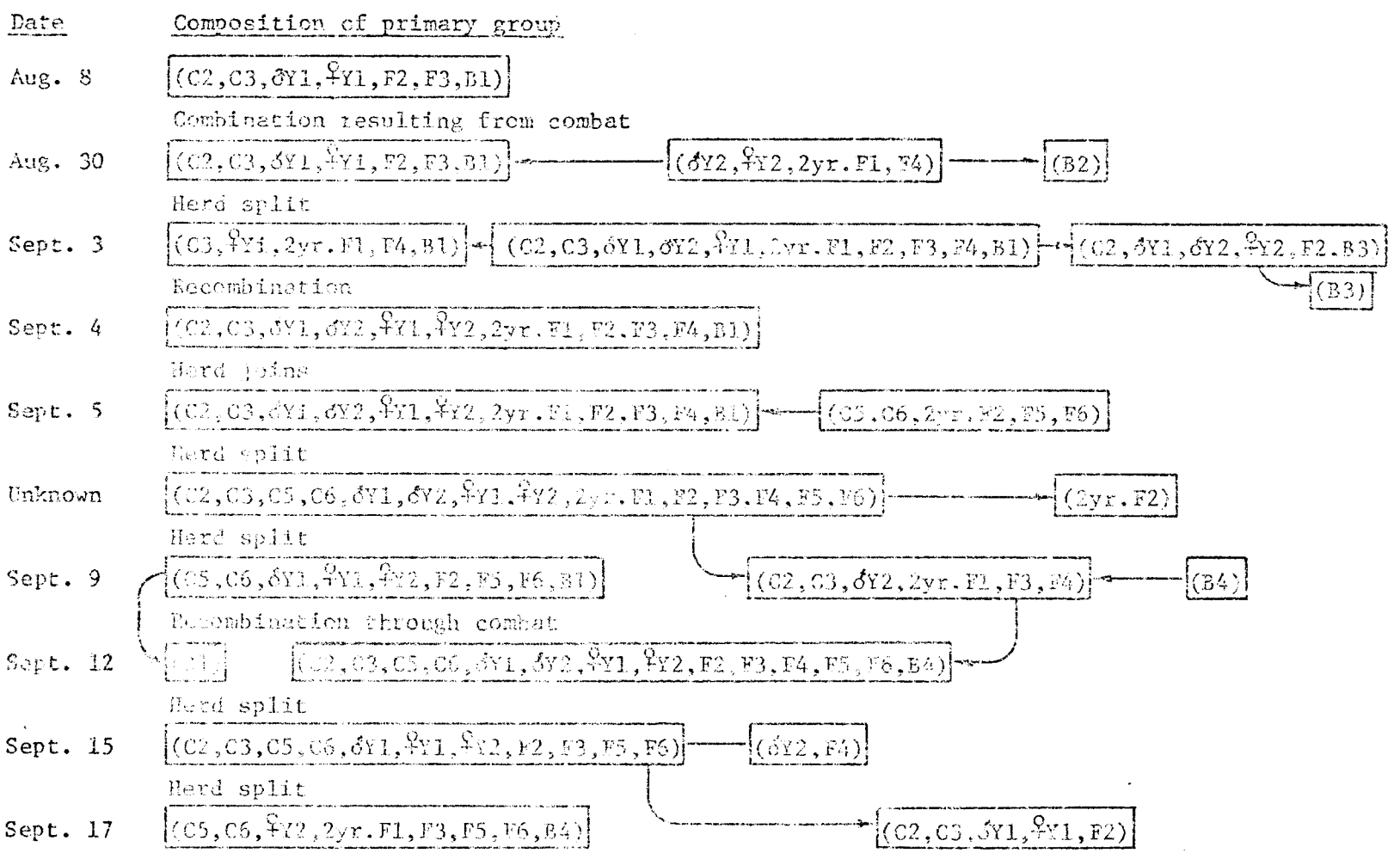
Fluctuations in Harem Size

Figure 33 shows the changes which occurred in the structure of one harem. The most common mechanism for increasing harem size was through combat between two harem bulls. Whenever harem groups moved into view of each other there was a general tendency for cows and juveniles to drift together. When the two groups had intermingled one of the two bulls had to be displaced. Usually the harem bulls met at a distance from the combined groups and after a series of agonistic displays, fought for possession of the herd.

The behavior of cows and juveniles following herd combination was similar whether the combination resulted from combat between bulls or not. Cows investigated one another sometimes showing components of male courtship patterns. Each age class tended to direct its investigatory behavior toward members of the same class in the new group or toward younger animals. Some aggression was seen between females during these initial encounters but attacks were not very serious.

As harems grew larger by combination they became increasingly

Figure 33. Harem size fluctuations.



LEGEND: C = Calf (calf's designation is the same as its mother's, i.e., C2-F2); Y = Yearling; 2yr.F = 2-year-old female; F = adult female; B = adult male.

liable to fracturing. As was previously mentioned, individual animals were hesitant to leave but groups were less reluctant to do so. Therefore fracturing usually resulted in the loss of several animals from the harem. Herd splits were not marked by any notable behavior. Large groups dispersed widely when feeding. In these feeding movements, one group of animals might move far enough to lose sight of the main group. Once this had happened they were as likely to continue on as to rejoin with the group. If these animals encountered a disturbance, however, their reaction was invariably to return to the main group. On two occasions I caused the recombination by exposing myself to the group which was without a bull. They immediately ran toward the rest of the harem, even though they had to run around me to do so.

Factors Influencing Harem Stability

The key factor which allows the harem to exist for a period of time is the desire of the cows to associate with others. Nevertheless, the bull does exert a major influence on the organization and stability of the harem. The incidence of fracturing is markedly reduced in the harem as compared to pre-rut herds. Although the average group size remained similar during either period (Table 4) the effect of the bull was to reduce the turnover rate. As the rut increased in intensity, the harem bull was constantly watchful for any movements away from the harem. As the size of the harem grew his requisite energy expenditure for controlling dispersal increased substantially. When harem size was between 5 and 10 active herding by the bull was not particularly

necessary. Although there were individual cows which appeared to have poorly expressed herd tendencies even these were not likely to leave the herd outright. However, when a harem grew to 10 to 15, if one cow left the group she was often accompanied by several others. Thus the subgroup provided reinforcement which satisfied the need for "fellowship" and permitted dispersal from the harem. One harem of 21 was seen but this probably exceeds the maximum number that the bull can control for long. Scattering was so common that this bull was constantly interrupted and prevented from performing extended courtship bouts. Altmann (1956a) reported a similar direct relationship between size and instability in elk harems.

The bull also exerts a strong stabilizing influence on the group's reaction to fright stimuli. Pre-rut herds were much less tolerant of disturbance and tended to take flight more easily than did harem groups. When a harem was confronted by a minor disturbance which caused the cows and juveniles to run, the bull often remained where he was or merely walked slowly after them. The sight of a casual reaction by the bull usually served to halt the others' flight. Frightened elk are quieted in the same way by the sight of peacefully grazing elk or even other species (Altmann 1956a).

A strong flight response to minor disturbance is counterproductive to courtship activity in that it disrupts the harem and creates an additional unnecessary energy drain. However, a reaction in which the animals remain in place but assume the defense formation serves to stimulate courtship. Gray (1973) observed the most intense sexual

interactions reported in his study following disturbance. Bull muskoxen engaged in active investigatory courtship when the harem was immobilized in the defensive formation. When faced with an unusual and frightening situation cows seemed to be oblivious to the advances of the bull. Bulls took full advantage of this to practice intensive testing.

Movements

During the summer, muskoxen moved about over an extensive area of suitable range. Daily movements were quite variable. A group might remain on one small area for several days, then suddenly travel 10 miles the next. However, a herd normally moved less than 3 kilometers a day. Figure 34 records the movements of a single harem over a 6-week period. Figure 35 shows the movements of two harems observed by P. Lent in 1969. The average distance between sightings one day apart for these three harems was 1.47 km or 0.91 miles.

Since movements are not always linear, these figures do not necessarily represent the actual distances covered. However, they do indicate that movements of this particular harem were generally short and confined to a relatively small area of the island. This generalization would not appear to be appropriate for all harems, though. It was my impression that even though groups might remain in one locale for a length of time, feeding movements were basically random and a fixed home range did not exist. Gray's (1973) data tend to support this idea. However, a full understanding of the dynamics of muskox herd movements and their relationship to home range must await further study.

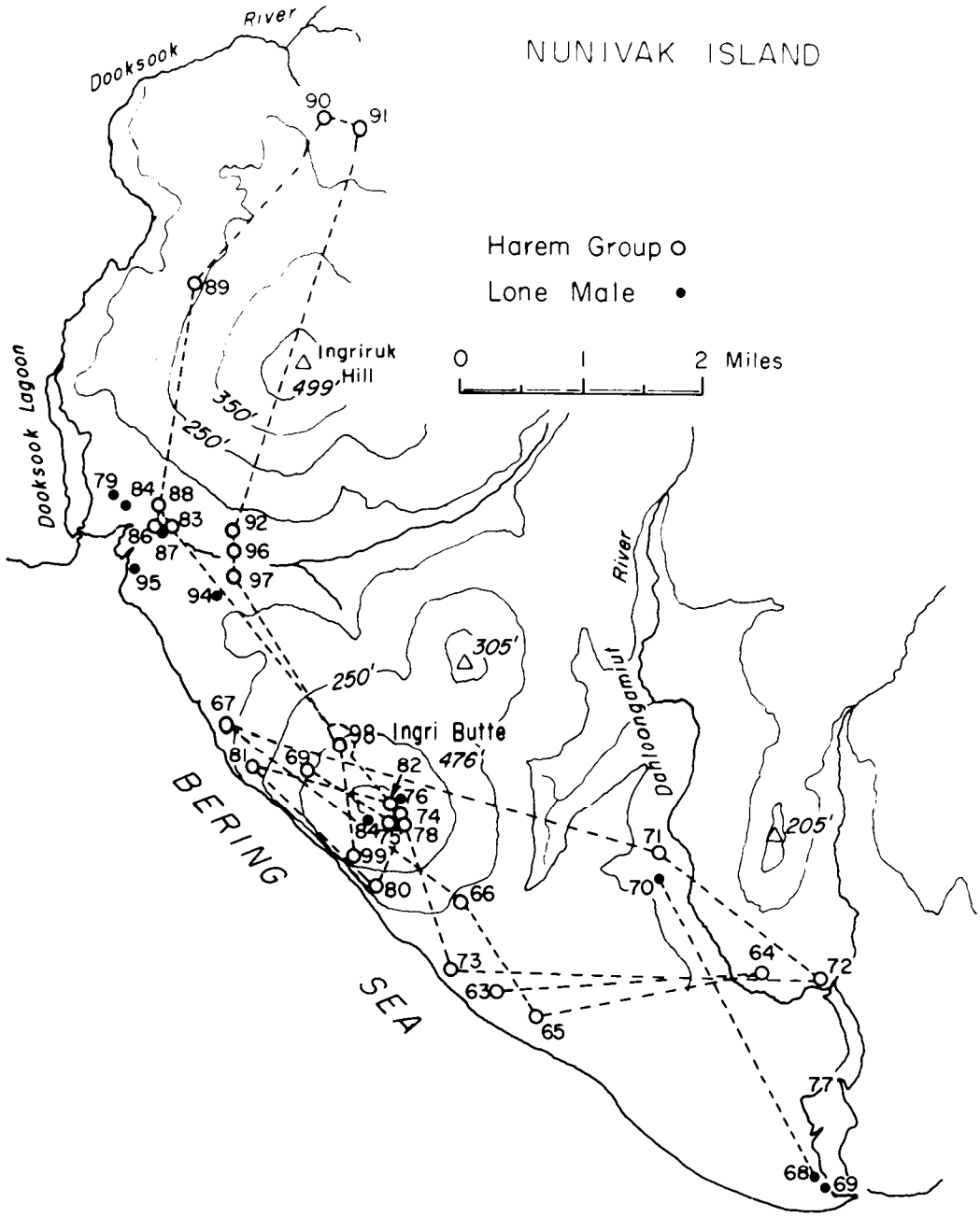


Figure 34. Movements of primary harem group and associated lone bulls observed in August and September, 1973. See table for details.

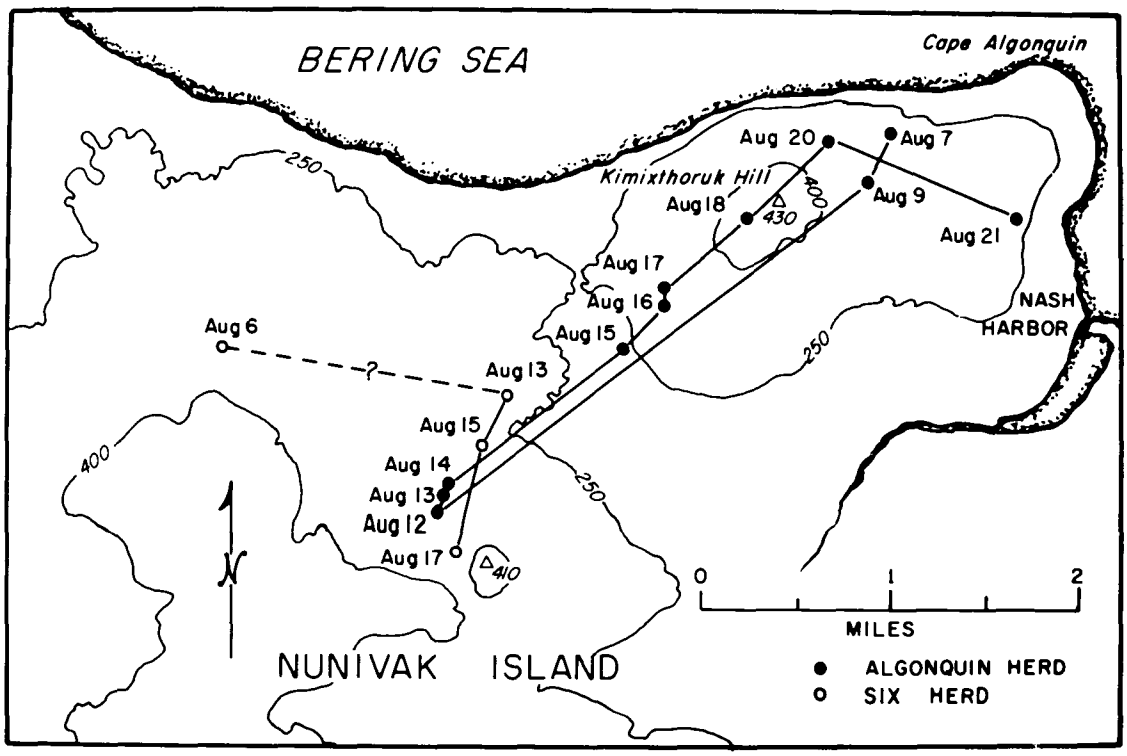


Figure 35. Movements of two harems observed in August of 1969.

Table 6. Group composition and dynamics during rut of 1973. Observation numbers correspond to those on map.

Date	Observation No.	Calves	Yearlings ♂	Yearlings ♀	2-yr-olds ♂	2-yr-olds ♀	3-yr-olds ♂	3-yr-olds ♀	4-yr-olds+ ♂	4-yr-olds+ ♀	Total	Remarks
8/12	63								1		1	Marked bull-yellow, broken horn M4
8/15	64	2	1	1					1	2	7	
8/16	65	2	1	1					1	2	7	Same as #64
8/21	66	2	1	1					1	2	7	Same as #64
8/22	67	2	1	1					1	2	7	Same as #64
8/24	68								1		1	Same as #63
8/25	69		1	1		1			1	1	5	
8/25	70								1		1	Same as #63
8/26	71	2	1	1					1	2	7	Same as #64
8/27	72	2	1	1					1	2	7	Same as #64
8/28	73	2	1	1					1	2	7	Same as #64
8/30	74 & 75	2	2	2		1			1	3	11	Groups 63 & 69 combined, B2 out
8/30	76								1		1	
9/1	77								1		1	Marked bull-red M10
9/2	78	2	2	2		1			1	3	11	Same as Group 75
9/3	79								1		1	
9/3	80	1		1		1			1	2	6	Part of Group 75, B1
9/3	81	1	2	1					1	1	6	Part of Group 75, B3
9/4	82	2	2	2		1			1	3	11	Groups recombined
9/5	83	2	2	2		1			1	3	11	
9/5	84								1		1	
9/5	85								1		1	
9/5	86	2		1						2	5	
9/5	87								1		1	

Table 6, continued.

Date	Observation No.	Calves	Yearlings ♂	Yearlings ♀	2-yr-olds ♂	2-yr-olds ♀	3-yr-olds ♂	3-yr-olds ♀	4-yr-olds+ ♂	4-yr-olds+ ♀	Total	Remarks
9/6	88	2	2	2		2			1	5	14	
9/9	89	2	1	2					1	4	10	Group 88 split
9/9	90	2	1			1			1	1	6	
9/9	91	2	1			1			1	1	6	Same as #90
9/12	92	4	2	2		1			1	5	15	#89 and 91 combined B1 out
9/12	93								1		1	
9/12	94								1		1	
9/12	95								1		1	Very old M17
9/13	96	4	2	2		1			1	5	15	
9/15	97	4	1	2		1			1	4	13	Bull of #89, 92
9/17	98	4	1	2		1			1	4	13	Same as #97
9/20	99	2	1	1					1	4	9	Part of #98 ?

Leadership

Although the concept of leadership is difficult to define, certain individuals do have a definite influence on the direction of herd movements. A leader is one who is frequently at the head of a moving column and often seems to initiate a new activity (Hafez et al. 1969b: 278). Unlike some wild sheep populations (Welles and Welles 1961) leadership is not the prerogative of any one individual in the harem. Muskoxen tended to follow any animal which made an initial movement away from he group. Members of all sex-age classes were seen in this role at one time or another. Leadership was also seen to shift during a single herd movement. This was particularly common when a young animal had initiated a movement. After leading for a while he often stopped and waited until an adult had replaced him at the head of the group.

In dealing with leadership and herd movements, it is necessary to distinguish three types of movement. These are:

1. Drift: Movements involving simple grazing patterns where leadership is absent or very unobtrusive. The group tends to move in synchrony but movements are basically undirected. Examples of leadership by juveniles and subadults were most commonly seen when these animals initiated a move to a nearby feeding area.
2. Directional "led" movements. Longer movements from one area to another which involved a definite leader. Animals grazed occasionally but steady movement of the herd was usually maintained. Cows ultimately led nearly all of these movements

though some of them were initiated by young animals. Occasionally two movements were started in opposing directions pulling the herd apart. In most cases one of the groups eventually reversed itself and followed the other.

3. Forced movements: Before taking flight from a frightening object the initial response was to run together into the classic defense formation. From here the animals generally broke and ran at top speed away from the threat. However, a number of aborted intention movements often preceded a stampede, particularly when the frightening object was first seen at close range. Situations which were perceived as dangerous tended to bring out the maximum expression of cohesion. And since fear provided strong stimulus for followership almost any animal could be a leader in these situations if he were able to leave the protection of the group. This appeared to be a difficult proposition even for those animals which had been regular leaders of previous herd movements. When one animal broke from the formation he was immediately followed by the rest of the group. However, after travelling only a short distance he often wheeled around to again face the object and caused the herd to reassemble around him. This sequence might be repeated several times with different animals leading before one continued on releasing a full-scale stampede.

In mass flight animals ran in a tight group with no apparent order or leadership.

Tener (1965) stated that an old cow led herd movements outside of the rut and that the harem bull was the leader during the rut. Gray (1973) reported his belief that bulls most frequently led group movements, particularly when the herd was confronted by an obstacle. Of herd movements observed during the present study where leadership was clearly evident, 86 percent were led by mature cows. The harem bull was only successful in leading one movement and a few were led by other bulls, calves, and subadults.

Differential effectiveness in eliciting a following response explains why cows were so often the leaders of herd movements. Though subadults made initial leading movements fairly often they were also very often ignored by the others. A cow could be expected to be followed at least by her calf and sometimes by other calves and yearlings associating with it. The sight of several animals moving was a much stronger stimulus for followership than a single individual.

The harem bull was generally more concerned with controlling dispersal and testing cows than in directing the movements of the herd. He actively worked to inhibit displays of leadership by herding wayward animals back into the group. On the few occasions when the harem bull did try to lead the group he was usually not very successful in getting others to follow him.

Hafez et al. (1969b) suggested that animals which are most frequently responsible for leading movements have a lower drive to associate than do those which tend to follow. Schein and Fohrman (1955) have shown that individual variation in cohesiveness exists in dairy

cattle and it was readily apparent that similar variation is present within a group of muskoxen. Animals with poorly expressed cohesive tendencies were generally older cows, cows without calves and animals newly introduced into the herd. Adult bulls seemed to be least affected by the need to associate.

Many unsuccessful attempts were seen to initiate movements, where an animal set off from the herd but his example was insufficient to cause others to follow. In these cases the cohesive tendencies of the leader, even though reduced, would eventually cause him to return to the herd.

By virtue of their independence, leaders were more likely to be lost from the herd. Although it was stated that individual emigration from a group was rare, three occurrences were seen. All of these (F1, F2, and 2-year-old F2) had poorly developed cohesive drives and strong inclinations to wander. F2 was the major leader of herd movements in one harem. Emigration from the herd is as much a result of the failure of the others to follow as it is an action of the principal animal. F1 and 2-year-old F2 made numerous intention movements but their success rate in eliciting a following response was low.

The relationship between social position and herd leadership has been discussed by a number of authors. Stewart and Scott (1947), Ross and Scott (1949), Beilharz and Mylrea (1963a, 1963b) and Dickson et al. (1967) concluded that in domestic cattle and goats leadership was related to social dominance but that there was no causal link. Geist (1971) found that dominance and leadership were positively correlated in some

mountain sheep bands but opposite in others. Tyler (1972) observed a certain relationship between dominance and march order in the New Forest ponies, but this was by no means consistent. Gray (1973:64) states that "Leadership in muskox herds is very closely related to the social dominance hierarchy, not only during the rut but throughout the year." Although I was unable to detect a stable social hierarchy within sex-age classes in rutting muskoxen, there was a definite dominance order between classes. The most dominant animal, the harem bull, rarely led herd movements. Conversely, the least dominant, a calf, could act as leader although this was also rare. Gray apparently based his conclusion on the observation that 10 of 15 herd movements were led by the dominant bull in a herd which contained three bulls and one cow. Although bulls are in fact dominant, they also have relatively low cohesive tendencies. Therefore Gray (1973) may have been confusing independence with dominance as the key factor which determines leadership. If dominance is related to leadership in muskoxen, the relationship is not direct and further work will be required to define that relationship.

Movements of Lone Bulls in Relation to Harems

The distribution of lone males and harem groups after the peak of the rut in September, 1971 is shown in figure 36. The map is based on the U. S. Fish and Wildlife Service survey report for that year. There was a general tendency for lone males to be found in the vicinity of harem groups as would be expected. Additional clumping of lone bulls not related to the distribution of harems was also seen, not only in

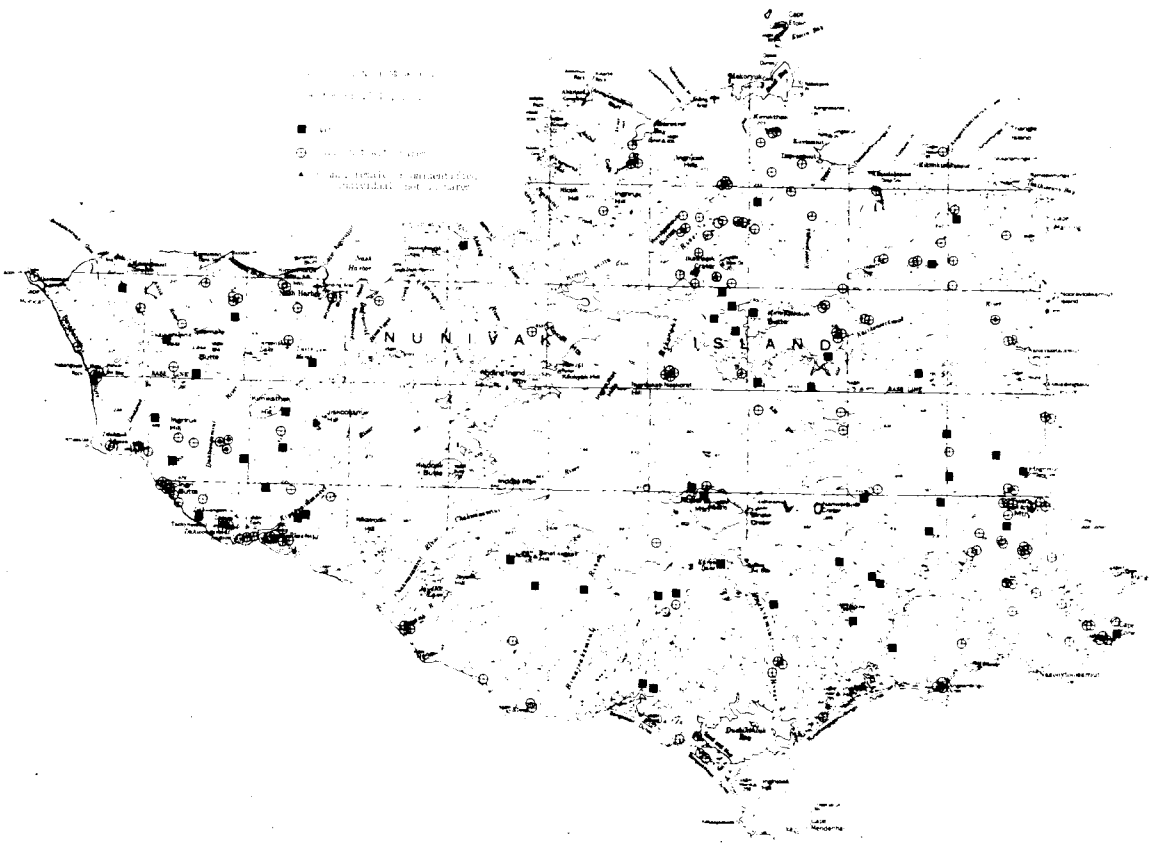


Figure 36. Distribution of muskoxen observed during the September 15-16, 1971, U.S.F.W.S. survey.

1971 but in 1969 (Lent 1974) and in 1972 and 1973.

In the fall of 1972 and 1973 harems were distributed along the coast with greater frequency than in 1971. Few harem groups were located in the interior during these years compared with 1971. During the 1972 and 1973 rutting seasons lone bulls moved along the coastal strip where the probability of encountering a harem was relatively high. Whenever one of these bulls sighted a harem group he moved to within several hundred meters of it and synchronized his movements with the daily feeding movements of the harem. After remaining thus on the periphery of the herd for as much as a day he eventually challenged and fought the harem bull. The loser of this contest then left the immediate vicinity of the harem and usually moved entirely out of the region.

In general, lone bulls had a higher rate of travel relative to the more stationary harem groups which resulted in a constant flow of lone males through the area occupied by the harem. This situation presented the harem bull with a continuously changing selection of challengers.

Bulls which were not in possession of harems often travelled together in pairs or small groups. The September 1971 U.S.F.W.S. census showed 170 bulls not associated with harems. Eighty-four occurred as lone individuals, 48 were in groups of 2, 30 in groups of 3 and 8 in 2 groups of 4 (U.S. Department of Interior 1975).

Social Hierarchies

Tener (1965:95) states that "A social hierarchy has been found in herds studied intensively and continuously," although he presented no

details to support this contention. Harington (1961) also suggested that a social hierarchy is present but again failed to provide data to justify his belief. Gray (1973) demonstrated a linear dominance order among three bulls and felt that similar hierarchies existed within all sex-age classes even though he was unable to document this. Although I agree with Tener's (1965) contention that there is a linear dominance order between sex-age classes (adult bulls dominate adult cows which dominate two-year-old cows which dominate yearlings which in turn dominate calves), I was unable to find a similar relationship within any particular sex-age group. In fact, in 208 hours of observation I only saw 17 instances of overt aggression between females. Of these, only 3 involved aggression between cows 4 years of age or older.

In the summer there are few resources which are limited enough to invoke individual competition. Therefore, there are few opportunities for the agonistic interactions which are necessary to establish a dominance order and even more important from my standpoint, to indicate its existence. If a dominance hierarchy is present within age classes of summer groups it may be a carry-over from the winter where animals are competing at feeding craters (Gray 1973). In any case there is little convincing evidence to either prove or disprove the existence of a stable dominance order within the harem beyond the one which was outlined above.

Agonistic Behavior

The rut brings out the most intense expressions of aggressive behavior seen during the year in most ungulates. Muskoxen are no exception to this rule. Battles between rutting males have left lasting impressions in the writings of such early authors as Hearne (1795), Pike (1892), Freuchen (1915) and Jennov (1933). Gray (1973) has provided excellent descriptions of general behavior patterns used in agonistic interactions. However, because the rut brings on marked changes in the level and frequency of aggression, additional commentary is needed to supplement his work.

The increasing intolerance between bulls associated with the rut has been described in earlier sections. As male hormone levels rise with the onset of the breeding season there is a corresponding rise in male aggressiveness and the incidence of agonistic interaction (Fraser 1968). The most serious demonstrations of aggression occur in combat for ownership of harems.

Threat Displays

A series of threats usually preceded combat. Bulls which had already met in several clashes often broke off and performed additional threatening patterns before proceeding with the battle.

1. Alert posture. When a harem bull first perceived a challenger, he faced him in the head-high posture which was described in the section on courtship behavior.

2. Head-low approach. As the bulls moved toward each other, they

walked in a determined stiff-legged approach with the head held low. This threat is similar to that described for domestic cattle by Fraser (1957) and Schloeth (1958) and for bison (McHugh 1958, Egerton 1964, Lott 1974).

3. Gland-rubbing. Bulls rubbed the pre-orbital gland against the lower part of the foreleg in agonistic encounters (Figures 38 and 39). This pattern has been described at length by a number of authors (Hone 1934, Pederson 1958, Tarasov 1960, Harrington 1961, Tener 1965, Gray 1973). Gland-rubbing will be further discussed in a later section.

4. Horning the ground. Bulls frequently horned the ground prior to combat (Figure 40). They tore out large chunks of sod with the horn tip and sometimes also pushed the horn boss and front of the face into the exposed soil.

5. Head-tilt. This was most commonly seen in association with the parallel walk. Bulls displayed broadside to each other and turned the head to face away from their opponent. A similar response to an antagonist is performed by male mountain goats (Geist 1964) and a number of other bovids (Walther 1974).

6. Parallel walk. Bulls often walked along parallel to each other for as much as 100 m holding the head tilt (Figure 41). They could either move in the same direction, opposite directions, or one bull might display to a stationary opponent.

7. Head-swing. After a clash, as the bulls backed, they pulled the muzzle in and swung the head from side to side in wide arcs (Figure 42).

Figure 37. Three-year-old cow in alert posture.

Figure 38. Adult cow gland-rubbing against driftwood.

Figure 39. Class 8 bull gland-rubbing against foreleg during a bout of threat display prior to combat with a harem bull.

Figure 40. Class 8 bull horning the ground.

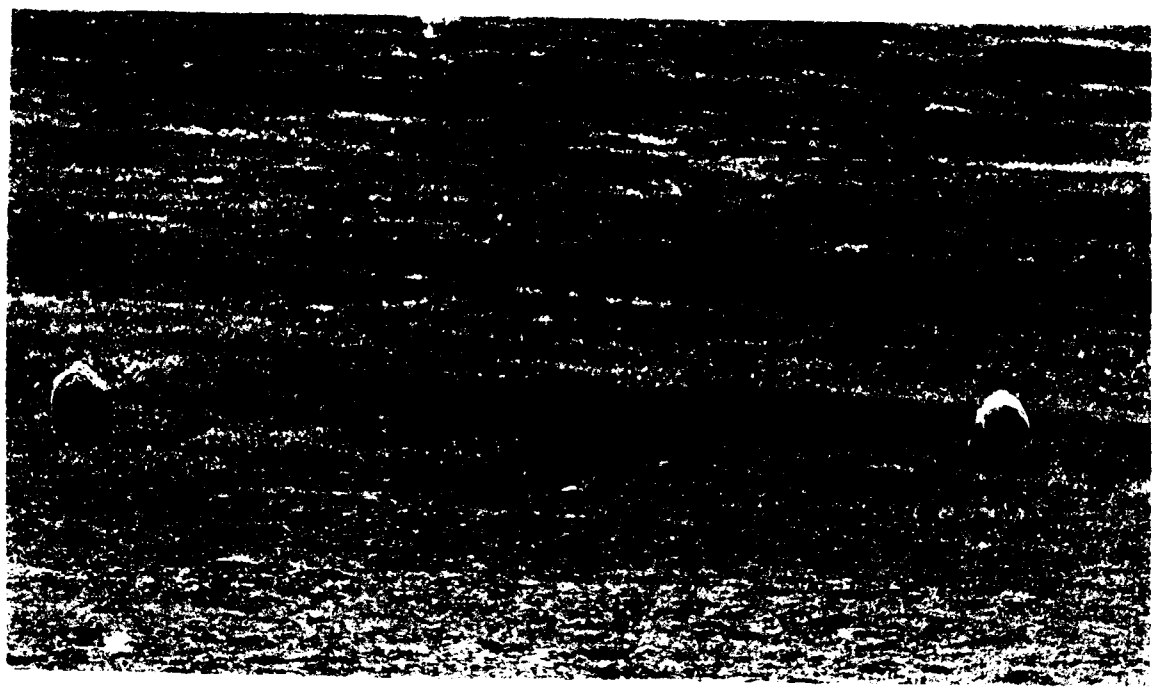


Figure 41. Harem bull and challenger performing parallel walk display.

Figure 42. Bulls backing after a clash performing head-swing.

Figure 43. The clash at impact.

The duration of threatening prior to combat was variable but usually lasted more than ten minutes. Sometimes a challenger moved away after a bout of threat display which did not lead to combat, only to return at a later time. One lone bull approached and displayed to a harem bull 5 times over a 7-hour period, each time moving off and feeding at a distance from the harem before finally engaging the harem bull in combat.

Bulls roared periodically throughout the threat display period. This vocalization was used in many other contexts than agonistic interactions though strangely enough Gray (1973) only heard it once. The roar is a deep guttural sound which to my ear was nearly identical to that made by a lion.

In this species threat displays do not seem to serve as a substitute for combat among mature bulls. When a lone bull approached a harem a dominance battle was almost a certainty. Threats may function to increase the confidence of the displaying animal and reduce the self-assurance of the recipient. In this way they may serve to limit the intensity of the battle. Bulls sometimes broke off fighting and retreated even though they had seemed to be holding their own in the clash.

The Clash

Combat between bulls may occur throughout the year and is particularly violent during the rut. The method of fighting is a head-on clash at high speed delivered and received on the horny carapace. Frame by frame examination of movie footage revealed the complexity of

this technique.

After the preliminary threat display the bulls ran toward each other from a distance of about 30 to 50 m. Sometimes the initiator began his charge while the other bull was still threatening. As the bulls approached they maintained head alignment so that the horn bosses would meet squarely upon impact. The frontispiece shows the intense concentration of bulls just prior to the clash. On the last step before impact, both bulls made a final lunge with the hind legs which lifted the forefeet off the ground. In the charge the head is held at mid-level with the face perpendicular to the ground. Immediately before clashing the bull pulled the muzzle back which threw the horn bosses forward and stiffened the neck for the blow. The hind feet remain on the ground, giving a solid skeletal connection from the horn boss through the spine and hind legs to the ground. The blow was caught simultaneously on both horn bosses and the force tended to push the head downward. After making contact the body continued onward compressing the neck. Often the back legs were thrown upward and forward, adding additional downward pressure.

The impact of the blow was tremendous (Figure 43). The sound, like a heavy timber being struck by a sledge hammer, could be heard for more than a mile. Bulls frequently rebounded 30 cm or more from the collision. During a clash muskox bulls generate forces which are probably unmatched by any other North American ungulate. The closing velocity of contestants in one clash was determined to be in excess of 10.9 meters per second or 24.4 miles per hour from movie footage. However, I consider this to be

a minimal figure for clash speed. Muskoxen can run 25 to 30 miles per hour on a hard snow surface (P. Lent 1973, personal communication) when chased by snowmobiles. My impression from witnessing many clashes was that bulls attempted to reach maximum speed which would produce a closing velocity of 22.34 m/sec or 50 mph. However, even at the lower figure, the impact is most impressive. Imagine the effect on an automobile undergoing 15 to 20 17-mph collisions against a concrete wall, which in terms of kinetic energy would be roughly equivalent to one battle.

Mountain sheep sometimes attempt to charge downslope to obtain maximum momentum (Geist 1971). Muskox bulls were not seen to take advantage of topography in this way. In fact, most battles were fought on level ground even though slopes were nearby.

After each clash, bulls faced each other for a short time then backed, swinging the head from side to side. When they were again separated by 30 to 50 m, one of the bulls initiated a charge and the clash was repeated.

Fights with as few as 4 clashes were seen but 15 to 20 was typical. Unusually prolonged battles might involve more than 20.

After a series of clashes one of the bulls began to show signs of impending defeat. Losing bulls were often slow to back up after a clash and ran a shorter distance in the charge, though this was not an invariable rule. The certain indication that the fight was soon to end came when one bull began to turn partially away from the other after each clash. Finally one of the bulls refused to meet the other's charge and was chased by his adversary. The loser continued to walk steadily away

from the harem until he was at least one or two km distant and usually did not even look back. Losing bulls were never seen to challenge the same harem bull twice. After disposing of his rival the victorious bull returned to the harem and often performed additional threat displays, tearing up the turf with his horns and roaring. Particularly aggressive sequences of courtship interaction were often seen following dominance battles.

Combat included much more variability than may be implied by the above brief description. Occasionally bulls engaged in pushing matches following a clash. Pushing was often quite vigorous but never decided a contest. Sometimes bulls clashed suddenly after backing only a short distance. The head swing serves to prepare a bull for such an attack. Beginning with the head pulled far to one side the bull snaps it forward as he lunges ahead with his whole body. In this way he achieves maximum velocity of the head though the body accelerates over a limited distance only. On one occasion following a pushing bout, two bulls became shifted around so that they were parallel, pushing against each other with the sides of their heads. Neither one could move away from the other without giving his opponent room to hook. Although they pressed the horn tips against each other, no apparent damage was done.

Attempts were made to attack the body or to stab with the horn, but these were generally unsuccessful due to the defensive actions of the recipient. Bulls defended against a charge by facing their opponent and catching the blow on the carapace. They were amazingly quick in their ability to do this, even when taken by surprise.

Physical Damage to Bulls from Combat

Although battles between mature bull muskoxen are decidedly vicious and grueling, there is little evidence of serious injury to the participants. Severe damage could be inflicted if the sharp horn tips were used to gore. However, bulls were very wary of body attacks and provided their opponents with few opportunities to use their horns in this way. I occasionally saw bulls momentarily lose the head to head orientation and bring the horn into contact with the other's neck or body, but they were unable to jab with much force and did not seem to inflict any damage. Tener (1965) maintains that bulls are occasionally gored in fights. The potential is certainly there, although I feel that this type of injury is unusual.

Direct concussion injury seems more likely. Following a series of clashes bulls often acted dazed. A harem bull that had fought several fights in a daily sequence bled freely from the nostrils and ears after each battle. This bleeding may have been due to the rupturing of sinuses in the skull. Freuchen's (1935) expedition found the skull of a bull which was split along the sagittal crest, apparently as a result of a dominance battle. A dehorned bull was killed in a rutting battle at the Institute of Northern Agriculture farm in Fairbanks. Death was the result of a shattered cervical vertebra (R. Dietrich, personal communication).

Old bulls were sometimes seen with part of the horn broken off. This injury was probably the result of combat and could involve major loss of blood if the horn core were damaged.

Old bulls were also seen with an opaque cornea on one eye. These could have been due to eye damage sustained in fights since the eyes are in a very vulnerable location. However, other explanations are equally feasible. They may be either an effect of old age or the result of insect harassment as reported by Palmer and Rouse (1936).

Physical Adaptations to Combat

Bull muskoxen have evolved a number of morphological adaptations in response to the needs of intraspecific combat.

Since most of the shock is taken on the head, it is here that the greatest modifications have occurred. The bone is heavily pneumaticized surrounding the brain case (see Figure 44). The target area delineated by the horn bosses, consists of about 10 cm of horn underlain by 8 cm of skull bone over the brain. The bull's skull is extremely massive when compared to the female's. Allen (1913) gives average weights of seven pounds (3.18 kg) for adult females and eighteen pounds (8.18 kg) for adult males. This is a 266 percent increase which can be directly attributed to sexual selection.

The first and second cervical vertebrae of the male and female are shown in figure 45. The males' first cervical vertebra transmits the impact from the skull to the spine which carries it deep within the body. The articulating surface of the male's atlas is 41.8 percent larger than the females', which offers obvious mechanical advantage. When the bull pulls back the muzzle at the final lunge, the atlas fits into a notch at the base of the occiput (Figure 44). This provides a very hard

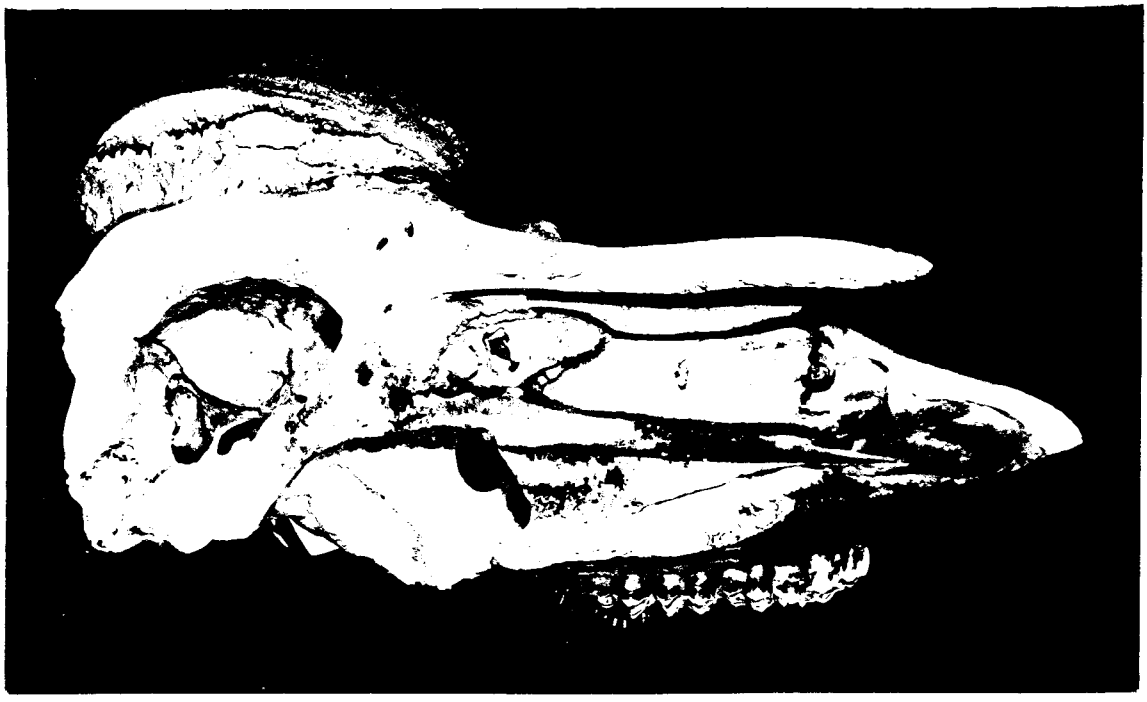


Figure 44. Sagittal section of the skull of a mature bull showing massive bone structure.

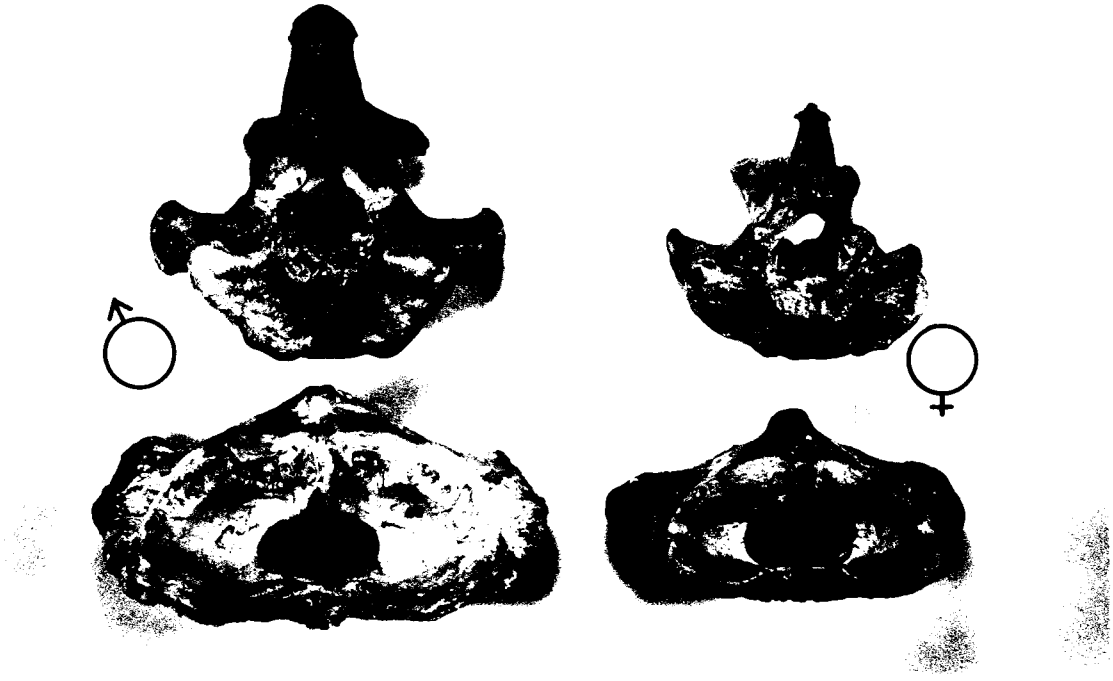


Figure 45. Comparison of first and second cervical vertebrae of mature male and female.

connection which maximizes the impact and at the same time places the horn boss directly in line with the spine so that the impact force does not tend to rotate the head up or down.

Males have powerful musculature in the neck to support the head and resist rotational forces at impact which could produce serious injury or death if unopposed (Schaffer 1968). Elongate neural spines on the cervical vertebrae provide additional areas for muscle attachment.

Reaction of Cows and Juveniles to Combat

The members of the harem seemed completely apathetic to battles for their ownership. Throughout the fight they continued to graze or rest, occasionally looking at the combatants but showing no great interest. On two occasions a harem moved away and left the bulls to fight alone.

Aggression by Bulls toward Cows, Sub-adults, and Calves

The bull was so clearly dominant over the other members of the harem that he needed to show very little overt aggression toward them. Bulls acted aggressively toward cows when herding them back to the harem and occasionally in courtship. Whenever the bull moved through the harem the other animals moved out of his way, watching him closely, ready to move further at any sign of aggression. Whenever a young animal was slow to move the bull displaced him merely by swinging his head or making a short charge in his direction. Often the bull chased calves away from their mother when he was courting her. At the peak of

the rut the bull became very intolerant of the yearling males in the harem though he had previously ignored them. Whenever he approached one of them at this time he chased the yearling out of the way, sometimes pursuing him for 20 or 30 m.

Aggression by Cows

Cows engaged in little active aggression. The most common expression of female agonism occurred when a calf attempted to nurse an unreceptive cow. The usual methods of repelling the calf was to swing the horns toward him in a sweeping arc. This was sufficient to chase the calf away though the blow rarely connected. Cows were surprisingly intolerant of other calves near their own and often chased them with no provocation. Aggressive interactions between adult cows were infrequent. Only 7 cases were recorded and in 4 of these aggression by a four-year-plus female was directed toward a two-year-old. The aggressive behavior itself was quite mild, usually not involving physical contact.

The most exceptional form of female aggression was between a cow and a mature bull. Only 2 examples of this were seen. These were discussed in the section on female sexual behavior.

Agonistic Behavior within Bull Groups

Relationships within bull groups during the rut were belligerent at best. Bull pairs were seen fairly commonly and seemed to be reasonably stable though the two bulls battled frequently. The existence of these strange associations seemed to be a result of two opposing

forces: the general cohesive tendencies of all muskoxen and the seasonal temperament of rutting bulls which leads them to regard approaching males as antagonists. This was brought out most vividly by the actions of a bull pair when exposed to a disturbance. The initial response of bulls in these situations was to run together, the typical muskox fright reaction. However, as they came together, instead of taking up defensive positions as usual, the bulls met in a clash. When further pressed they took flight, but after running a short distance, the lead bull wheeled around and met his partner in another head-on clash. This continued until the animals had moved away from the disturbance. I often caused lengthy battles between bulls merely by walking toward them. Apparently bull muskoxen react to any running approach by another bull as an intended attack. The appropriate defense against an attack is to meet the blow and neutralize it against the horn bosses.

Battles between non-harem bulls differ from fights for possession of harems in several ways. Fighting for a harem was a formal, ritualized affair which was carried on with few interruptions until a definite winner emerged. Individuals in bull pairs often grazed between bouts of combat and the fight usually ended indecisively with the two simply wandering apart.

Scent Marking

Muskoxen possess a pair of well developed pre-orbital glands that secrete an odoriferous substance which may function in olfactory

communication. One of the ways these glands are used involves a highly stereotyped and dramatic display: gland rubbing (Figures 38 and 39). When gland-rubbing the displaying animal extends the foreleg and rubs the face up and down against it, presumably depositing pre-orbital gland secretions with each motion.

The motivations for gland rubbing and its function have been areas of discussion and conjecture for previous authors (see Hone 1934, Pederson 1958, Tarasov 1960, Harington 1961, Tener 1965, Gray 1973). Gray (1973) has presented a review of the past hypotheses regarding gland rubbing along with an original one which depicts its major importance as being a visual display.

In conformity with Ralls' (1971) precept that scent marking is the prerogative of the dominant animal, bulls gland-rubbed more frequently than cows. Cows performed this behavior on only two occasions.

In addition to auto-marking, muskoxen rub their pre-orbital glands against pieces of driftwood, Eriophorum tussocks and newly horned patches of earth (Figure 38). I watched several bulls horning the ground within 5 m of me. Each time they used the horn to tear into the ground they rubbed the side of the face on the soil which had been uncovered. Bulls sometimes additionally rubbed the front of the face and horn boss onto the same area. These places carried a faint sweetish odor, different from soil which had not been so treated. In the threat display period before a fight both bulls horned the ground repeatedly, turning up patches of torn sod over the prospective battlefield. Following the defeat of his opponent, the victor often moved to each of the places

which had been horned by the loser, sniffed them and horned and rubbed his face against them, which suggests individual recognition of scent marks.

Ralls (1971:443-444) has stated that animals "mark frequently where they are both intolerant of and dominant to other members of the same species. In other words, they mark when they are likely to attack another member of the same species, and are likely to win if they do attack." This would seem to apply to the scent marking which was done by muskoxen.

Often when a harem moved into an area which it had not occupied for some time, the harem bull was seen to horn the ground in the absence of threat stimuli. Thus it seems that bulls may scent mark as a regular procedure on new areas that the harem occupies. Additional high intensity marking is performed in the presence of a contender. Scent marking in the latter situation may serve to intimidate the opponent and stimulate the performing animal to attack (Ralls 1971).

Play Behavior and the Ontogeny of Sexual and Agonistic Behavior

Muskoxen spend comparatively little of their time in play. Typically, play was restricted to young animals. Table 7 shows the age classes of animals engaging in bouts of play behavior. Only 6 of the 47 observations involved adults. There is a tendency for yearlings to play with yearlings and calves with calves (Table 7). Calves and yearlings tended to associate with members of their own age class more frequently than with others in activities besides play also.

Table 7. Age classes of animals engaging in play.

Class of Animals	Number of Observations	
	Alone	Social
Adult	2	0
Adult with Yearling	---	4
Yearling	3	30
Yearling with Calf	---	5
Calf	1	12

General sexual and agonistic behavior patterns were displayed by young calves early in the spring. As Geist (1971) suggests, animals may be born with the basic patterns of clashing and mounting and acquire the more elaborate details with age and experience.

As rutting behavior began to occupy increasing importance in the lives of adult animals there was a corresponding increase in the number of sexual and agonistic patterns used in play. In the late summer both calves and yearlings performed mounting with pelvis thrusting, chin up, head swing, horning the ground and head tilt. Figure 46 shows how the peak occurrence of these behaviors in play coincided with the height of rutting activity among adults. Young animals may either be incorporating behavior associated with the rut in their daily activities through imitation or they may be affected by changing hormone levels in the same way as adults.

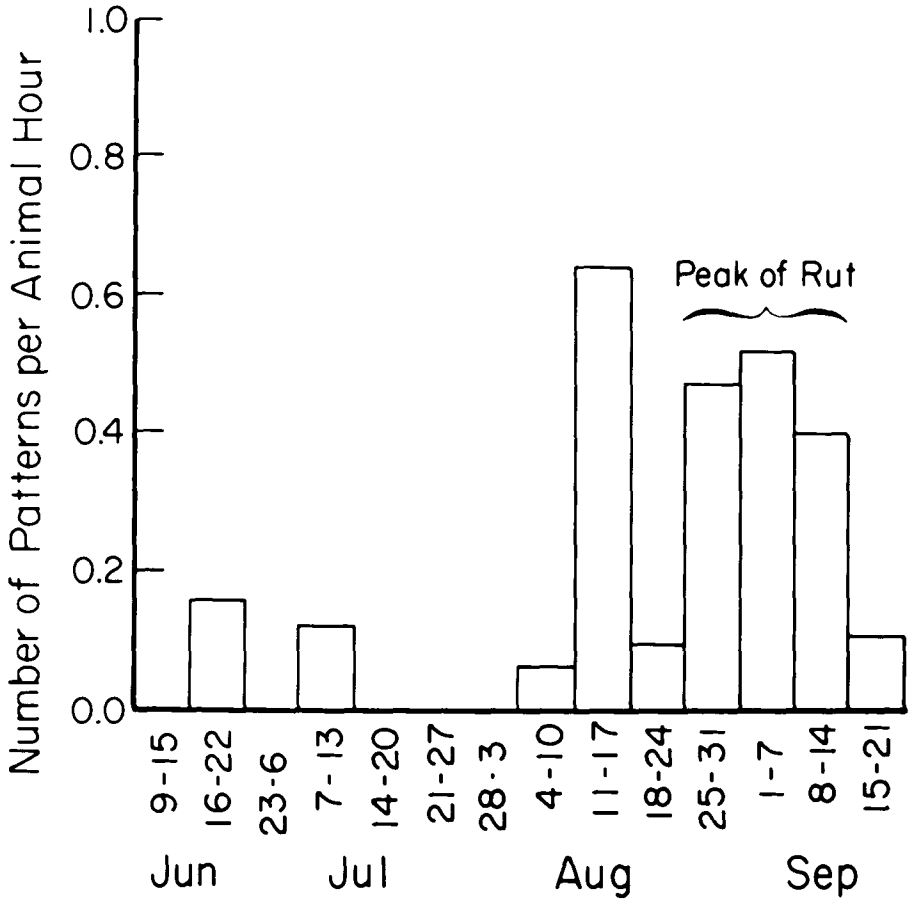


Figure 46. Frequency of sexual and agonistic patterns performed in social play.

FINAL DISCUSSION AND CONCLUSIONS

The Functional Significance of Courtship

Sexual reproduction, in its simplest terms, involves a transfer of genetic materials between two individuals of a species. Courtship ritual has evolved for the sole purpose of facilitating this transfer. The proper performance of courtship behavior assumes major importance in allowing the deposition of viable sperm within the female reproductive tract at the proper stage of her estrus cycle.

Walther (1974:84) has pointed out three behavioral problems which must be dealt with before copulation can take place. (1) The male must overcome the female's reaction, either flight or aggression, to his close approach. (2) He has to maneuver her into the subordinate posture necessary for copulation. (3) The female has to overcome the males aggressiveness and prevent him from treating her as a defeated conspecific. Thus courtship requires a delicate balance between aggressiveness and submission which is determined by the environment and social system of the species. Geist (1971) differentiates between "rough" and "cautious" male courtship behavior and discusses factors which regulate levels of male aggression. In many species, aggression is required to make the female receptive to the male (Ewer 1968). However, undue aggression is maladaptive in that it may either cause the female to withdraw or to respond with an attack. Muskox courtship is

intermediate between the violent behavior of the Camelidae and the extreme caution shown by certain territorial antelopes.

Males of species which exhibit cautious courtship behavior (mountain goat, mountain sheep: Geist 1964, 1971) have developed an approach posture for use in sexual contacts which is the antithesis of their offensive display. According to Geist, these have developed in the case of goats to avoid a dangerous attack which could kill or cripple the male and in the sheep to prevent the ewe from running from the ram. Male muskoxen do not have a comparable display to communicate their intentions in a sexual approach. The absence of a display may be due to the fact that unlike goats, for example, female muskoxen are hardly capable of causing severe injury to the males of their species. Furthermore, since the harem system encourages regular contact between the bull and cow for a long period of time before cows come into estrus, females become accustomed to the bull's approach and learn to react in an appropriate manner. Nevertheless, the harem system selects against undue levels of male aggression because these would be destructive to the harem itself. The gradual courtship seen in muskoxen tends to preserve the integrity of the harem by avoiding sudden changes in the relationship of the bull toward the cows.

In short, the major function of the extended courtship period in muskoxen seems to be to allow the cow time to habituate to the presence of the bull. Courtship also provides immediate reward for the bull which reinforces his drive to maintain the structure of the harem over the period prior to copulation.

Implications of the Harem Social System

Muskox social organization changes considerably due to the rut. Closed harem groups are in major contrast with the open structure of muskox herds throughout most of the year.

Many of the gregarious ungulates employ variations of the harem breeding system: red deer (Cervus elaphus, Darling 1937), elk (Cervus canadensis, Altmann 1952, 1956a, Struhsaker 1967), chamois (Rupicapra rupicapra, Altmann 1956b, Krämer 1969), plains zebra (Equus quagga), mountain zebra (E. zebra), and Asiatic wild ass (E. hemionus) (Klingel 1974), horse (E. przewalskii, Tyler 1972, Klingel 1974), Grant's gazelle (Gazella granti, Walther 1965) and non-migratory reindeer (Rangifer tarandus, Espmark 1964) to name a few. These species cover a broad range of taxonomic groups and inhabit widely varying habitats, yet all possess similar breeding systems.

Orians (1969) maintains that polygyny is always advantageous to the male. Downhower and Armitage (1968) have shown that in certain cases increasing numbers of females in the harem actually reduces the relative fitness of the male by introducing female competition. They contend that for their study population, monogamy is the optimal female strategy. In muskoxen neither of these latter contentions apply. It is advantageous for a bull to breed as many females as possible, as Orians suggests. However, there are certain qualifications which must be made. The physical pressures imposed on the harem bull are somewhat proportional to the number of cows in his harem. Bulls go into a negative energy balance during the rut. Teal (1959) and Hubert (1974) have shown that

bulls lose weight steadily throughout the period of the rut even in captivity. Figure 28 shows how the time allocated to feeding and resting declined and was superseded by courtship activity. Herding behavior places a significant demand on the bull's energy reserves, particularly as harem size increases. When this energy drain is added to the requirements of intraspecific combat (which is not a function of harem size) the total demand may be extreme. In fact, it is possible that a very fit bull who takes possession of a harem early in the season may be so exhausted by the demands of the rut that he could be defeated by a lesser bull. If a bull expends too much energy during the rut he may enter the winter in such a depleted state that his chances for survival would be reduced. If his probability of obtaining a harem in the following year is low, then his best strategy would be to maximize his reproductive effort in the one year even though it might result in his death. However, if there is a chance that he will be permitted to breed in subsequent years, then he should be expected to limit his energy expenditure in order to maintain sufficient physical reserves to compete the next year. Since the demands of intraspecific combat are beyond his control, the only way he can vary energy requirements is in his herding effort. Because larger harems will fracture without the constant attention of the bull, the amount of energy the bull is able to allocate to herding imparts an upper limit on the size of the harem.

Females benefit from polygyny in several ways. By mating with a bull which has proven his ability to dominate other males they increase the probability that their male progeny will acquire the traits which

are essential for male competition. In this way, by increasing the odds that their male offspring will reproduce, they enhance their own relative fitness. During the rut herd behavior is also important from the standpoint of predator defense and calf survival as it is at other times of the year. Gray (1973) has shown that muskoxen in groups are essentially invulnerable to wolf attack unless they take flight. As I stated in preceding sections the harem bull tends to stabilize the herd's fright response and inhibit stampedes.

The harem system is particularly suitable for muskoxen because they are normally found at very low densities. Since breeding groups are established well before cows come into estrus the chances that a fertile cow will not have access to a bull are decreased.

Because the dominant male is constantly monitoring the female throughout her estrus cycle two of the general problems of courtship -- the detection of estrus and the synchronization of male and female behavior -- are easily accommodated. This is reflected in the fact that females do not display elaborate signs of receptivity.

The Harem as Territory

Noble (1939) gave the following simple definition regarding territorial behavior: "territory is a defended area." Burt (1943, 1949) accepted this but expanded upon it to distinguish territory from home range. "Home range is the area usually around a homesite, over which the animal normally travels in search of food. Territory is the protected part of the home range or only the nest. Every kind of animal may be

said to have a home range, stationary or shifting, only those that protect some part of the home range by fighting or aggressive gestures from others of their kind during some phase of their lives, may be said to have territories" (Burt 1943.35).

Carpenter (1958) in an excellent review of the concept recognized the great variability in the behavior among the diverse groups which display it and suggested that territoriality be viewed "primarily as a behavioral system which is expressed in a spatial-temporal frame of reference." Harem defense would seem to fit into the general framework of territorial behavior. Espmark (1964) and Ewer (1968) both ascribe territorial attributes to the defense of a harem. The important aspect of territoriality is not that a specific geographical area is controlled but, as Graf (1956) points out, the fact that an individual of a species recognizes a space as his exclusive property and restricts access to it.

Seen in this light, scent marking by muskoxen takes on a new meaning. Animals with fixed territories often use scent as sign posts to delineate their territories. The function of these sign posts is to intimidate encroaching members of the same species. Bull muskoxen mark their own bodies by gland-rubbing them when an intruder enters the area around the harem. It is common knowledge that territorial animals are more likely to win fights on their own territory. Therefore, this type of marking may act as a reassurance that he is on home ground. Although gland-rubbing no doubt has more than one meaning (see Gray 1973) the analogy to territorial marking is striking. Male reindeer respond in a very

similar manner by depositing strongly scented urine on the hind legs when another bull approaches the harem (Espmark 1964).

Sexual Selection and the Harem Bull

Muskoxen are species which exhibit strong sexual dimorphism. Data on weights of animals collected in the wild are scarce, partially due to the difficulties of weighing large animals under field conditions. Wilkinson (1973) reports that mature cows are two-thirds the weight of mature bulls. According to the Jarman-Bell hypothesis (Jarman 1968, Bell 1971, as cited in Geist 1974), optimum body size for an ungulate species is a function of forage quality and abundance. Since both sexes exploit the same food resource, one would expect that they would have evolved similar proportions if environmental factors were the exclusive determinants. Given Amadon's (1959) premise that body size of females is a reflection of environmentally imposed selective pressures it would appear that the increased size of males may actually be detrimental to the survival of the individual.

Because only a small minority of bulls are able to breed, acquisition of a harem assumes paramount importance. Harem bulls exert a disproportionate influence on gene frequencies in the population. Thus it can easily be seen why selection would have favored traits which are necessary for reproductive success even at the expense of environmental adaptation.

Males would experience greatest difficulties in winter when both sexes have a reduced forage resource available to them, because they

must maintain a substantially larger mass on that forage. Since both sexes have similar grazing and digestive efficiencies (Hubert 1974), the unmet energy requirements of bulls would be proportionately greater. Since adult males may be one-third larger than adult females (Wilkinson 1973) in order for the net energy balance to be equal for both sexes, either the energy required per kilogram for maintenance of males must be much lower or their gross energy intake must be greatly increased. It is unlikely that energy requirements would differ in this way between sexes. In average winters it also is unlikely that bulls would be able to increase their intake of forage sufficiently to make up the difference. Hubert (1974) has shown that during the months of January, February and March on Devon Island bulls lost weight at a greater rate than did cows, even though many of the cows were pregnant. Thus it would seem that bulls might be at a relative disadvantage in mild winters where fairly extensive feeding areas were available and competition was insignificant. However, when winter forage was very restricted, their physical strength and dominance could allow them to displace females from feeding areas and monopolize the limited food source.

That sexual selection can impart non-adaptive characteristics was demonstrated by Selander (1965) for the great-tailed grackle.

Orians (1969) has argued that mate selection is the primary force which determines which male will breed which female or females. In muskoxen it appears that selectivity is of minor importance and that male competition is the major mechanism which is responsible for mate selection. From a behavioral standpoint two factors determine the

relative fitness of a bull muskox (assuming equal ability to produce fertile matings): (1) the ability to acquire a harem; and (2) the ability to defend it against competitors and natural dispersal until cows are bred. Characteristics which are appropriate to these goals and consequently should be selected for are (1) large body size, (2) efficient weapons for intraspecific combat, and (3) high levels of male aggression. These three traits are under selection by male competition.

Body weight is of great importance due to the muskox's mode of fighting. From a theoretical growth curve Hubert (1974:59) has suggested that bulls attain maximum body weight at six or seven years. This coincides with the average age of the harem bull which was obtained in the present work. Thus it would seem that the best competitor in muskox combats, the harem bull, has reached his maximum weight yet is still young enough to possess speed and agility. Geist (1971) compared the techniques used in sheep combat to that of a practitioner of karate. Intraspecific battles in muskoxen can be more aptly compared to sumo wrestling. The antagonists strive to accelerate mass maximally and throw it against their opponents. In muskox fights as in sumo, large body size offers an unmistakable advantage. The precise timing and exquisite use of the horns Geist (1971) describes for sheep are not present in muskox fights. They are simple exhibitions of mass and power.

The horns have evolved as the exclusive organs of combat in the muskox. Overall the horns are similar in both sexes, which implies that they serve a comparable function in both. Males and females both

have the sharply pointed, upcurving shaft which is used against the animal's principal predator, the wolf. Long association between these two species has produced in the muskox an efficient weapon which combined with appropriate defensive tactics offers a formidable protection against attack by wolves (Gray 1973). Both caribou and muskoxen inhabit similar environments. Both have evolved under predation by wolves. However, caribou run from wolves while muskoxen stand and face them. This difference in predator defense strategy is probably due to the larger body size of the muskox which allows them to battle wolves successfully (Geist 1974).

By its structure the horn would appear to be best adapted to sideways, stabbing movements. The observations of Macmillan (in Allen 1913) and Pederson (1958) of defensive techniques against sled dogs confirms this. The behavior of muskoxen when threatened is to back together and present the potential attacker with the heavily armed head. When alone they sometimes back against banks of earth or boulders. When a group is faced with threats from several sides this tendency to face outward results in the classic circular defense formation.

Males have developed an extra process on the horn which is of little importance in interspecific defense. That is the thickened horny carapace at the horn base. This structure receives the impact of the blow in male dominance battles. Allen (1913) reports that maximum deflection of the horns in bulls is reached at four years. However, bone deposition at the base of the horn cores is most active at five to seven years, coinciding with the period of most active male competition

for harems.

Thus the horn of the muskox can be considered to comprise two distinct weapons. One which is possessed by both sexes is a truly lethal weapon to be used against predators. The second, found only in bulls, serves to protect the head from the extreme force of the clash.

Two sets of behavior have developed for use in inter- and intraspecific agonistic encounters. Geist (1966) considers that head to flank lateral engagements such as those used by present-day mountain goats represent primitive ungulate fighting methods. Vicious fights in this manner could be expected to cause serious injury or death to one or both of the combatants. Consequently, animals such as the mountain goat (Geist 1964) have developed social displays which reduce actual fighting. Because of the great difference in the fitness of harem owning and non-harem owning muskox bulls, male competition assumes paramount importance. However, as Geist (1971, 1974) points out, damaging intraspecific combat is particularly non-adaptive for species such as muskoxen which have low replacement rates.

Thus we see a compromise in the evolution of weapons and defensive behavior to reduce injuries during conflict. In animals which use the head-flank attack a thickened dermal shield has been developed over the vulnerable areas of the body. Muskoxen have weapons which are as deadly as those of the mountain goat, yet they have abandoned the lateral shield and the offensive flank attack.

It is not altruism on the part of the attacker which makes muskox

contests relatively bloodless. Rather, it is the skill of the defender. Bulls are very accurate in catching their opponent's charge with the horn boss. If in pushing, the horns lose contact, they wheel around to prevent him from gaining the head-flank orientation which would allow him to hook. Furthermore, a bull which is in a position to use the horn tip against his opponent's flank is vulnerable to a similar attack.

Thus it can be seen that muskoxen have achieved a virtual elimination of physically damaging combat without sacrificing the utility of their weapons. Mountain sheep have evolved morphological and behavioral adaptations which reduce damage in intraspecific combat but in the process, have reduced the effectiveness of their horns against predators.

The Role of Lone Bulls

Polygyny restricts breeding to a small minority of bulls. This leaves a large number of adult males in the population which are unable to acquire harems. In the 1973 population estimated at 532 (Lent 1974) there were only about 50 to 60 harem bulls. This meant that 135 to 145 mature bulls were not directly responsible for breeding. What then is the importance of this group to the population?

The muskox social system is set up in such a way that it acts as a rigorous sorting mechanism for male characteristics. Lone bulls provide a pool of genetic variability which is necessary for selection. The more adult bulls in the population, the more intense the competition for harems. Even during the rut when segregation of breeding from

non-breeding males is at its greatest it cannot be assumed that those which are not with harems are not important to the reproduction of the species. Much interchange of harem bulls takes place throughout the rut and a bull which is with a harem at a particular time is not necessarily the one which will serve the cows. The popular conception that lone bulls are all old senile individuals is patently false (Table 5). A bull which is alone early in the rut may breed in the next year or even later on in that year. Reducing the male population to the minimum required for reproduction would weaken this social selection mechanism and may help to maintain hereditary traits in the population which would have been strongly selected against under normal conditions.

It has been argued in the past that adult sex ratios on Nunivak have become abnormally skewed in favor of males (Spencer and Lensink 1970). In order to test the validity of the basic premise (that sex ratios are in fact abnormal) it is necessary to compare them to data from other muskox populations. Unfortunately, little usable information is available. There are no data at all for Greenland populations (Poul Henrichsen 1974, personal communication). Published information on Canadian muskoxen is presented in table 1. These figures must be regarded with certain reservations. Complications inherent in the basic data such as small sample size, failure to define which animals are included in adult categories and the problems associated with summer surveys which leave many animals unclassified and tend to miss lone bulls, make interpretation difficult. Gray (1973) arrived at ratios of 123:100 considering animals four years and above in his study

population on Bathurst Island. Hubert (1974) on Devon Island found ratios of 109:100 in 1970 and 119:100 in 1971 considering bulls four years and older to cows three-years-plus. My own data from the summer of 1973 show adult sex ratios of 115:100 and 106:100 comparing the same age groups. Recent information from Nelson Island which contains an increasing population derived from transplants off Nunivak also shows a predominance of males.

Looking at the available data there is no justification for the assumption that adult sex-ratios on Nunivak are unusually shifted in favor of males. Free ranging populations may display sex ratios which differ slightly from equality in either direction.

In actual significance for reproduction, the Nunivak population may be even less skewed than Canadian populations with similar composition. Because cows breed at 2 years of age and frequently produce calves in successive years (Spencer and Lensink 1970, Lent 1974), the proportion of sexually active females to bulls in any one year may in fact be higher than it is in areas where female fertility is not so great.

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