ALASKA DEPARTMENT OF FISH AND GAME
DIVISION OF GAME
Federal Aid in Wildlife Restoration
Final Report

STATUS AND DISPERSAL OF AN INTRODUCED MUSKOX POPULATION ON THE SEWARD PENINSULA

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Projects W-22-3, W-22-4, W-22-5
Job 16.1R
September 1987

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FINAL REPORT (RESEARCH)

State: Alaska

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Project No.: W-22-3 W-22-4 W-22-5 Project Title: Big Game Investigations

Job Title: Status and Dispersal of an Introduced Muskox Population on the Seward Peninsula

Job No.: 16.10R

Period Covered: 1 July 1983-30 June 1986
(Includes data through January 1987)

SUMMARY

The holarctic distribution of muskoxen (Ovibos moschatus) was severely reduced at the end of the Pleistocene and the beginning of the Holocene, primarily as a result of human predation. In North America the decline continued into historical times and threatened the survival of the species. Muskoxen were reintroduced to formerly occupied range on the Seward Peninsula in 1970 and 1981. The initial phase of growth of this population was poorly documented but incidental sightings indicated widespread dispersal. Aerial photography of muskox groups that included radio-collared individuals was tested as a means of censusing the population. A census could be obtained with 6% of the population instrumented. This method proved to be cost effective compared with the random transect visual surveys used previously. Various drugs and delivery techniques for immobilizing muskoxen were tested. It was concluded that carfentanil citrate (Wildnil, Wildlife Laboratories, Ft. Collins, Co.) was the most effective drug available. A trained Australian cattle dog was used to hold a herd in a defense formation for darting. This method was superior in every respect to helicopter darting. Various methods for visual marking of muskoxen were evaluated. Muskoxen were more mobile, on the average, than moose which were also studied on the Seward Peninsula. No evidence to support the existence of isolated, cohesive groups within the muskox population was found.

Key words: Chemical immobilization, home range, mortality, movements, muskox, Ovibos moschatus, population identity, radiotelemetry, Seward Peninsula, transplants.

CONTENTS

BACKGROUND

Muskoxen (*Ovibos moschatus*) are among very few survivors of a diverse ungulate fauna which inhabited North America during the Pleistocene. In northern Alaska, where at least 15 genera of large herbivores occurred during the glacial period (Guthrie 1972), only 4 (each represented by a single species) remain: caribou (*Rangifer tarandus*), moose (*Alces alces*), sheep (*Ovis dalli*), and muskoxen. At the beginning of the present century, it was clear that unless effective action was taken to reduce human-caused mortality, muskoxen, which had already been extirpated from Alaska, would become extinct.

Muskoxen were probably subjected to the same pressures responsible for the depletion of the holarctic megafauna at the end of the Pleistocene. Several authors have argued that predation by primitive man was the agent primarily responsible for the abrupt wave of extinctions in the late glacial and early Holocene, and man appears to have been the proximate cause of the extinction of muskoxen in historic times in Asia (Vereshcagin 1967) and Alaska (Steffanson 1921). Reduction of habitat appears to better explain the much earlier extinction of muskoxen in Europe (Kowalski 1967).

Muskoxen survived in North America when so many other species failed probably because of their adaptation to environments that were extremely difficult for man to colonize, and the time required for hunting societies to develop technologies which allowed exploitation of the extreme north. The pattern of overharvest which would ultimately have led to the extirpation of muskoxen from North America and Greenland was well established prior to the arrival of western European society, but social and economic changes brought by westerners definitely increased the rate at which the species was forced toward that end. I agree with Steffanson (1921) and Hone (1934) that primitive hunters had both the technology and the proclivity to bring about the extinction of the species in North America and Greenland as they had in most of their former range.

In Canada, the development of a market for muskox meat and hides in the early 19th century, and indirectly, the development of the fur trade led to a drastic increase in the slaughter of muskoxen. In Greenland, these factors and the practice of killing all adults in a herd to obtain calves for European zoological gardens resulted in an alarming decline in muskox numbers (Hone 1934, Pedersen 1958).

The coming of the fur trade into the north meant that native hunters who had formerly followed caribou migrations or moved out onto the sea ice to hunt seals remained in northern interior areas during the winter. The need for large dog teams for commercial trapping, and the marketability of muskox skins and skulls greatly increased the demands placed on muskox populations in areas which had formerly been refugia. After the decimation of the plains bison herds, hide hunters moved north and naturally shifted to muskox hunting and trapping. Increasing numbers of whalers, traders, exploration parties, and other Caucasians wintering in the high Arctic added considerably to the pressure on muskox populations through their own hunting, by employing native hunters to supply game meat for humans and for dog food, and by providing a ready market for meat and hides.

History of Muskoxen in Alaska

Not surprisingly, considering the very recent nature of written history in northern Alaska and the logistic limitations imposed on early historians, it is impossible to reconstruct the historic demography or demise of muskoxen in Alaska. However, Brower (1911) reported that when he first went to Barrow in 1884 there was an old Eskimo there who had killed muskoxen with a bow and arrow. Another informant told him how as a young boy his family had spent a spring on a tributary of the Kuk River near Wainwright in about 1858 (Steffanson in Allen 1912). It was a period of famine in the region and the man's father killed many muskoxen for his family and saved meat to give to others who were starving. This account typifies the use of muskoxen as a buffer species by hunters who normally were dependent upon seals or caribou in the pattern suggested by Burch (1977). Reed (1946) related accounts of muskoxen being killed as late as 1892-93 between Christian Village and the Sheenjek River and of another herd killed east of Chandler Lake in the winter of 1897-98 or 1896-97 by French-Canadian trappers. Regardless of the actual date of extinction, it is apparent that the extirpation of muskoxen in Alaska occurred over a long period of time and that isolated populations may have survived until very recently.

Probably no other extant large mammal is as vulnerable to hunting as the muskox; the universal practice in hunting them was to hold a group in place with dogs and to kill every animal in a herd (see Hone [1934] for a review). Capture and marking techniques used in this study and previously (Smith 1976) have demonstrated that muskoxen can easily be struck by arrows or hand-thrown projectiles and that an entire group can be held in place indefinitely while any or all animals are struck. The introduction of firearms was not the pivotal event in the demise of muskoxen, as many authors have maintained. In fact, some native hunters continued to rely on spears or arrows to kill muskoxen even after they had obtained firearms, in order to save limited supplies of powder and shot for more elusive game (Burch 1977). Ray (1975) reports that firearms were not widely available to Alaskan natives until the middle of the 19th century when widespread trade with whalers developed. It is apparent from the absence of first-person literary accounts of muskoxen in Alaska that the species was uncommon by that time. Although the last muskox in Alaska may have been killed with a bullet, muskox numbers were probably severely reduced by overharvest much earlier.

By 1929 it was apparent that no muskoxen remained in Alaska, and the dismal outlook in Canada and Greenland indicated the need for effective conservation measures to prevent worldwide extinction. In 1917, Canada amended the Northwest Game Act to provide full protection to muskoxen. However, ineffective enforcement and continued harvest under exceptions to these regulations, and the lack of protection in Greenland (Pedersen 1958), put survival of the species in doubt.

With these concerns in mind the Alaska Territorial Legislature petitioned Congress to acquire a herd of muskoxen from East Greenland and to use them as breeding stock in restoring viable populations in Alaska. Through the efforts of Senator Norbeck of South Dakota, Representative Dickinson of Iowa, and Alaska Game Commission member Irving McK. Reed, Congress appropriated $40,000 in 1929 to carry out this program. The sequence of events leading to the reestablishment of muskoxen in Alaska is unprecedented in early wildlife conservation efforts.

Nunivak Island was designated as a National Wildlife Refuge primarily to provide a range for the muskox population which would produce animals for introduction to the Alaska mainland. In the 1929 executive order (E.O. 5095) which established the Nunivak Refuge, President Hoover set forth the objectives of the muskox program. This order, the legislative history of the appropriations bill, and Palmer and Rouse (1936) established the goals for reintroducing muskoxen to Alaska:

1. "To aid in conserving a species threatened with extinction." (Palmer and Rouse 1936)

2. "For contemplated experiments in reestablishing the muskox as a native animal in Alaska." (Hoover, E.O. 5095 [1929])

3. "For experimentation with a view to their domestication and utilization." (Norbeck 1928)

History of Muskoxen on the Seward Peninsula

It is impossible to reconstruct the distribution and densities of aboriginal muskox populations. However, skeletal remains indicate that muskoxen were widely distributed in Alaska. Russel (1898 in Allen 1912) believed that muskoxen were once abundant from the Mackenzie Delta to Bering Strait. During the last several thousand years, muskox populations were probably heavily influenced by man and their distribution severely restricted. Therefore, I consider assertions by a number of authors, (e.g., Spencer and Lensink 1970) that the arctic coastal fringe be considered historic muskox range to be valid only in a very restricted historical sense. These authors stated that for indigenous muskox populations in Alaska, "there was no apparent barrier to the southward dispersal of muskox except for increased snow depth and prevalence of icing conditions along the coast of the Bering Sea," and suggested a correlation between recent distribution patterns and regions of low precipitation. Their analysis completely ignores the destructive impact of the human population. Precipitation may, in fact, provide a limiting constraint at some point, but experimental evidence indicates that annual precipitation isobars which could be expected to limit muskox survival occur much further south than those proposed by Spencer and Lensink (1970:12).

The success of recent introductions irrefutably demonstrates that muskoxen do not require extreme high-latitude habitats. In fact, observations of higher rates of productivity and survival on more southerly ranges (Smith 1976, 1981; Jingfors and Klein 1982) indicate that high arctic environments may not even be optimal.

Buckland (Appendix in Beechey 1831), professor of geology at Oxford University, examined the skeletal material collected by Beechey's expedition (1825-28) at Elephant Point on Escholtz Bay on the northern Seward Peninsula. He stated emphatically that the muskox bones were of recent origin and not from the same period as the mammoth and rhinoceros bones also recovered by the expedition. Although Beechey did not encounter living muskoxen on the coast, he interviewed a man from a party of natives who lived "some distance" up the Buckland River; the man's familiarity with the species suggested that muskoxen either still survived or had only recently been exterminated.

The causes for the recent extinction of muskoxen on the Seward Peninsula, whether due to predation or to changes in the environment, can be debated ad infinitum, but success of the current population most graphically demonstrates the suitability of the area for this species today.

Muskoxen were transplanted to the Seward Peninsula in 1970 and a supplemental transplant was made in 1981 when the population numbered about 100 (Smith 1984b). Sex-age status of the transplanted animals is shown in Table 1.

This report summarizes available data since the 1970 introduction and more intensive study conducted since 1983.

OBJECTIVES

This study was not funded at the level originally authorized, due to competing Regional priorities. Consequently, the scope and expectations of the project were reduced; these findings represent research carried out at a more modest level than

Table 1. Sex-age status of muskoxen transplanted to the Seward Peninsula from Nunivak Island in 1970 and 1981.

Age	4 years +		3 years		2 years		1 year		
Sex	M	F	M	F	M	F	M	F	Total
1970				2	3	1	16	14	36
1981		1[a]		3		1	10	22[b]	37
Total									73

[a] Fell through sea ice and drowned immediately after release.

[b] Yearling female suffered capture myopathy. Not released.

originally proposed. Availability of funding from the National Park Service during 1986-87 will allow this work to be continued.

The revised objectives are as follows:

1. To develop methods for censusing the Seward Peninsula muskox population and to test methods for censusing muskox populations elsewhere.

2. To determine if discrete subpopulations or persistent associations of individuals occur.

3. To acquire quantitative information on aspects of home range, movements, productivity, mortality, and social structure of the Seward Peninsula muskox population.

4. To develop improved methods of capturing and marking free-ranging muskoxen.

STUDY AREA

The Seward Peninsula is approximately 53,000 km^2 (20,463 mi^2) in area and extends from the northwestern coast of Alaska into the Bering Sea. Topography varies from coastal lowlands to rugged mountain ranges with a maximum elevation of 1,438 m (4,714 ft).

The climate is strongly influenced by surrounding water, and temperature, rainfall, snow, and icing conditions are typical of maritime areas in northwestern Alaska. The climate of the Peninsula's interior is more continental, with greater temperature extremes and lower precipitation. Mean annual precipitation is approximately 36 cm (14 in), measured at Nome. Snowcover normally persists from November through May and can be hard-packed and include ice layers, particularly near the coast.

Windswept mountainous terrain, even though sparsely vegetated, is important winter habitat for muskoxen on the Seward Peninsula, primarily because of its tendency to retain less snow than the lowlands. Isolated rounded or flat-topped hills with surfaces composed of small pieces of frost-shattered rock and soil, interspersed with both xeric and mesic tundra plant communities, are preferred. These areas may be used by muskoxen during any part of the year but are of primary importance during winter. Productive mixed-plant communities in the raised depressions formed by melting of the ice lenses underlying pingos are important winter and summer habitat on the northwestern portions of the Seward Peninsula. These areas are used intensively until snow becomes too deep for foraging. The mountainous habitat described above is the final refugia when snowfall restricts access to most Seward Peninsula range. Muskox/snow-cover relationships have been discussed previously by Smith (1984a).

MATERIALS AND METHODS

Muskoxen were captured for marking with the use of immobilizing drugs. A variety of drugs and methods were tested (Table 2, Table 3). Syringe darts manufactured by Palmer (Palmer Chemical and Equipment Co., Douglasville, Ga.) and by Pneudart (Williamsport, Pa.) were used to administer capture drugs. Long-range powder projectors made by Palmer and Zoolu Arms (Omaha, Nebr.) were used to propel the darts. Muskoxen were darted from a helicopter or from the ground. Helicopters, fixed-wing aircraft, and snowmachines were used to transport capture personnel to the vicinity of muskoxen.

Muskoxen were variously marked with metal ear tags; large, plastic, cattle ear tags; visual collars; plastic streamers attached to the horns; and VHF radio collars (Telonics, Inc., Mesa, Az.).

Blood was collected (with blood collection needles) directly into evacuated tubes (Vacutainer, Becton-Dickinson, Rutherford, N.J.) or into a 50 cc syringe and then into evacuated tubes. Plain tubes were used to collect blood for serology. Whole blood was stored in tubes containing powdered heparin or EDTA. Serum was sent to the National Veterinary Services Laboratory in Ames, Iowa, for screening for disease antibody titers. Hematological values were measured by the Norton Sound Regional Hospital in Nome, or by the investigator.

Muskoxen were given intramuscular injections of antibiotic (Flocillin, Bristol Laboratories, Syracuse, N.Y.). Dart punctures were inspected for imbedded hair or foreign matter and treated with nitrofurazone powder (Furacin, Morton-Norwich, N.Y.).

Muskoxen were aged using criteria developed by Smith (1976). Males to 5 years and females to 4 years could be accurately aged; beyond these limits, muskoxen were assigned relative ages based on horn development and other age-related physical changes.

Radio-collared muskoxen were relocated on a monthly schedule, from a fixed-wing aircraft. The search area was expanded, as required to locate all of the radio collars, on each series of

Table 2. Drugs used alone or in combination to immobilize muskoxen on the Seward Peninsula, 1982-86.

Chemical name	Trade name	Supplier
Etorphine HCl	M99	Lemon Co., Sellersville, Pa.
Carfentanil citrate	Wildnil	Wildlife Laboratories, Fort Collins, Colo.
Xylazine HCl	Rompun	Haver-Lockhart, Shawnee, Kans.
Acepromazine maleate	Acepromazine	Fort Dodge Laboratories, Fort Dodge, Idaho.
Hyaluronidase	Wydase	Wyeth Laboratories, Philadelphia, Pa.

Table 3. Drugs used alone or in combination to reverse the effects of immobilization drugs.

Chemical name	Trade name	Supplier
Diprenorphine HCl	M50-50	Lemon Co., Sellersville, Pa.
Naloxone	Naloxone	Wildlife Laboratories, Fort Collins, Colo.

relocation flights. The group which included a radio-collared animal was visually sighted at each location. Numbers of animals in the group and in the immediate area were recorded on field data sheets. The number of calves and the sex-age status of other identifiable individuals were recorded. Habitat type, time and date of observation, and the identity of marked animals associated with the group were also recorded. Locations were marked on 1:63,360 USCGS topographic maps in the field and transferred to individual movement-record maps stored in Nome. Field data were recorded on a permanent individual movement record using dBase III software (Ashton-Tate, Culver City, Calif.).

Reports of sightings of muskoxen on the Seward Peninsula were solicited through local radio spots, articles in the local newspaper, and public notices.

RESULTS AND DISCUSSION

Visual Marking of Muskoxen

All of the animals transplanted from Nunivak Island were marked with numbered metal ear tags (Table 1). Muskoxen transplanted in 1981 were additionally marked with color-coded plastic flagging (Safety Flag Co., Pawtucket, R.I.) attached to the ear with the metal ear tag. Five adult cows transplanted in 1981 were fitted with radio collars and numbered yellow visual collars (Appendix A).

An ideal method for marking muskoxen for individual visual identification under field conditions remains to be found. On Nunivak Island in 1973, I marked adult bulls with breakable plastic bags of powdered fabric dye hand-thrown against the animal, and also experimented with glass balls attached to arrows shot from a bow and a line projector using blank cartridges to carry the dye longer distances. In 1979 and 1980 I marked 30 muskoxen on Nunivak Island with numbered red cattle ear tags (T-Lock Tags, Hasco, Inc.); 1 muskox was marked with yellow tags. Miller et al. (1977) marked 22 muskoxen in a single group by aerial spraying of dye. Jonkel et al. (1975) reported on a variety of marking methods tested on Bathurst, Devon, and Ellesmere Islands including paint, plastic and metal ear tags, plastic streamers fastened to the horn, and numbered radio collars. Reynolds et al. (1982, 1984, 1985) used colored plastic streamers attached to the horns with metal hose clamps in northwestern Alaska. Clausen (1984) used cattle ear tags and paint on the horn boss to mark muskoxen in Greenland.

In this study muskoxen were marked with visual collars, numbered red T-Lock cattle tags, and color-coded plastic streamers attached to the lower curve of the horns with adhesive under sections of heat-shrink plastic tubing tightened with a propane torch.

Ear Tagging:

Of the methods I have observed, only the cattle ear tags appear to provide adequate sightability and durability for a long-term study. Red was the most visible color, of those available from the manufacturer. Yellow tags contrasted poorly with muskox pelage coloration and were extremely difficult to observe. Fluorescent colors probably would be more visible but were not available. The tags used were 5x7 cm and inserted into the anterior surface of the ear. They could usually be seen from the air but were not always readily distinguishable. The numbers were never visible from the air and the lack of availability of a selection of usable colors precluded color coding. The numbers usually could be read by an observer on the ground using a spotting scope.

Ear Tags and Streamers:

Plastic streamers fastened with ear tags were readily visible from the air and could be color-coded for identification of individual animals; however, they were not durable and most were tattered or lost after the 2nd winter. Apparently, none survived 3 winters. Cattle ear tags used on Nunivak Island were still readable after 8 years.

Horn Streamers:

Streamers fastened to the horns were very easily sighted from the air and could be color-coded for individual recognition. However, none of the animals retained them longer than a few months. In every case, the heat-shrink tubing remained on the horn and the streamer itself was lost. Unfortunately, the heat-shrink tubing was less visible from the air than ear tags and could not be used for individual recognition. Reynolds (1985) reported similar losses of horn streamers from her marked animals. Gray (1979) observed the animals marked with horn streamers and hose clamps described in Jonkel et al. (1975) for behavioral studies and his reference to identification of individuals by the presence of hose clamps implies that his animals experienced similar losses of horn streamers. Although I have not observed muskoxen attempting to rid themselves of horn streamers, I suspect they were scraped off on soil and rocks in ground-horning behavior, as described by Smith (1976). Since the streamers are in the animal's field of vision, muskoxen may consciously attempt to remove them.

The high visibility of horn streamers makes them a desirable alternative if better materials can be found. Metal hose clamps potentially could cause disfigurement by constricting growth of horns, and if placed too high on the horn shaft could put pressure on the living horn core. Since heat-shrink tubing proved to be durable and is not likely to have these effects, it is the preferred method of attachment.

Visual Neck Collars

Yellow plastic and fabric collars, 15 cm wide with 13-cm-high black numbers, were used unsuccessfully as marking devices. The collars were usually covered by the long guard hair of the neck and shoulders. When animals were crowded together in a defense formation, as was often the case when a group was observed from an aircraft, the collar was additionally blocked by other animals. For these reasons, visual collars were almost never visible from the air and were even difficult to see from the ground. Furthermore, the guard hairs tend to bunch up under the collar and probably cause the animal discomfort.

Radio Collars

Radio collars were the primary means of relocating marked individuals although the devices could rarely be observed from the air or from the ground. The collar material was a sandwich of fabric-reinforced butyl rubber machine belting sewn to a belt of urethane-reinforced fiberglass.

Radio longevity was variable with muskoxen studied on the Seward Peninsula (Table 4). Two radios are still transmitting after 69 months. Eight of 24 radios failed short of their expected 36-month operational life. Six of the 8 radios that failed were on males, although 13 males and 11 females were instrumented. Male muskoxen must subject radio transmitters to more abuse than females. It has been suggested that the mercury switch used as a mortality sensor may be broken by the severe impact of clashes between bulls (Stan Tomkiewicz, pers. commun.). Batteries are also sensitive to shock. Smith (1976), using frame-by-frame analysis of motion picture footage, determined a closing velocity between bulls, during a clash, of 10.9 m/sec; the energy generated is equivalent to an automobile colliding with an immovable barrier at 27 km/hr. Since a dominance battle may include 20-30 clashes it is no wonder that some electronic components expired.

Muskox anatomy does not lend itself to collaring. The profile of the neck at the base of the skull may be nearly even with, or higher than, the horns. If the collar is put on loosely it may slip forward over the horns and face as reported by

Table 4. Radio transmitter failures in muskoxen radio-collared on the Seward Peninsula, 1982-86.

Months of operation	Sex	Date collared
19	F	06-82
21	F	10-83
15	M	04-84
21	M	10-83
22	M	04-84
12	M	10-83
30	M	08-83
2	M	04-84

Reynolds (1985). This occurred with 1 animal collared in 1981 and transplanted to Seward Peninsula. Muskoxen should be fitted with tight collars. If animals are thin or still growing, some space for growth must be allowed, but loose collars invite serious problems. Once a collar has slipped over the face and horns it is unlikely that the animal can return it to the normal position, and even if it does, the collar will probably slip again. The potential for collar slippage makes collaring young animals questionable.

Capture Methods

Early methods of live-capturing muskoxen involved killing all adults in a herd and capturing the young animals with lariats or by hand (Hone 1934). Most of the 382 muskoxen handled for transplants or live-capture operations on Nunivak Island were captured by hand or with a large mesh net. The 30 muskoxen I marked and released in 1979 and 1980 on Nunivak Island were captured by tackling animals younger than 2 years from a snowmachine or by lassoing adults. The assistance of Nunivak Island residents experienced in handling muskoxen captured in transplant operations made this a practical, if not hazard-free, method. It took 7 men to throw 1 large bull which had been lassoed. Manual capture is best attempted in deep, soft snow. The target animals can be cut from the herd with snowmachines and will take a stand more readily when escape is impeded by snowcover. Occasionally a muskox that does not respond to immobilizing drugs must be physically restrained; a lariat is an indispensable tool for drug capture operations.

Anderson (1966) made reference to use of the drug curare to pacify adult bulls during the process of capture of calves. Alexander et al. (1968) reported on the use of succinylcholine chloride (Anectine, Burroughs-Wellcome Co., Research Triangle Park, N.C.) alone or in combination with propiopromazine HCl (Tranvet, Diamond Laboratories, Des Moines, Ia.) to immobilize muskoxen on Nunivak Island. Jonkel et al. (1975) used succinylcholine chloride and promazine HCl (Sparine, Wyeth Laboratories, Philadelphia, Pa). Both authors reported long periods of incapacitation and a number of mortalities. Jones (1971) was able to handle a captive adult bull muskox sedated with xylazine.

Recent efforts to capture free-ranging muskoxen with drugs have relied on the extremely potent, synthetic, morphine-like compounds, etorphine HCl (Dieterich 1970; Patenaude 1982; Reynolds et al. 1982, 1984, 1985; Clausen et al. 1984) and carfentanil citrate (this study) alone or with a synergist. The advantages of the synthetic opiates for immobilizing free-ranging animals are: rapid onset of catatonia, a wide range of tolerance in ruminants, and the availability of antagonists to rapidly reverse the effects of the drug. Unlike the curare-like muscle relaxants, the synthetic narcotics are both neuroleptic and analgesic in effect and are therefore superior for humanitarian reasons.

When used alone, both etorphine and carfentanil produced severe hypertonicity and moderate convulsions in muskoxen. Acepromazine and xylazine were used in combination with the narcotics to mediate and reduce these undesirable side effects. Muskoxen immobilized with carfentanil-acepromazine experienced some elevation of body temperature. A maximum rectal temperature of 106.8 F (normal - 101.2 F [Patenaude 1982]) was measured for an animal which had been chased more than a mile in deep snow before being darted. Ambient temperature was 15° F.

Clausen et al. (1984) reported successful immobilization of 487 muskoxen in East Greenland with use of a standard adult dose of 2 mg etorphine, 30 mg xylazine, and 200 IU hyaluronidase, although some variation in effectiveness was experienced and several animals required an additional dart. Dieterich (1970) reported an effective dose of 0.0125 mg/kg for captive animals or 3.5 mg for a hypothetical 280-kg adult. H. C. Hopf (in Patenaude 1982) recommended 7 mg of etorphine for cows and 8 mg for bulls, based on experience with captive animals. Patenaude successfully immobilized captive muskoxen using 2.2-3.0 mg/100 kg etorphine and 1.0 mg/kg chlorpromazine or 6-8.5 mg etorphine for a 280 kg adult bull. Reynolds et al. (1985) used doses of 4 to 26 mg etorphine with xylazine to immobilize free-ranging muskoxen in the Arctic National Wildlife Refuge, Alaska. From 1982 to 1986 I immobilized 33 muskoxen using etorphine, xylazine, and hyaluronidase. Initial etorphine doses ranged from 7.5-8.5 mg for adult cows and 8.5-9.5 mg for adult bulls. Both sexes were given 35 mg xylazine and 250-350 IU of hyaluronidase in the initial dart to facilitate absorption. Induction times ranged from 5-18 minutes for animals that went down with a single dart. Some animals required 1 or more additional darts and remained mobile for as long as an hour.

Etorphine performed erratically for immobilizing muskoxen in the current study. Jessup et al. (1985) concluded that bighorn sheep are insensitive to opioids, and capture efforts in this study suggest that muskoxen are as well. The successful use of much smaller effective etorphine doses by other workers, particularly Clausen et al. (1984), is difficult to reconcile. Captive animals typically respond to smaller drug doses than wild animals since drugs can be administered under ideal conditions, but the large number of animals successfully handled in Greenland by Clausen, who used similar materials and methods of administration, is perplexing.

Etorphine is currently supplied in the United States in concentrations of 1 mg/ml. The use of 1 mg/ml etorphine on muskoxen necessitates using 10-cc syringe darts which perform poorly when fully loaded, both ballistically and in their ability to fully inject their contents. Darts were observed to yaw in flight and on at least 1 occasion a dart ejected before reaching the animal. On several occasions the plungers of 10 cc darts were not forced completely to the end of the dart barrel by the internal charge, and part of the dose remained in the dart. Even when the darts struck in a large muscle mass and fully injected their contents, the large volume of fluid may not have been fully absorbed. Powder-actuated syringe darts eject their contents with explosive force. Such rapid injection of fluid may damage capillary circulation in the immediate region of impact and could create a pressurized bolus of liquid within the muscle tissue. The liquid could then pass back out through the needle channel. On occasion I noted the drug leaking from needle wounds after animals were immobilized.

After experiencing repeated problems in immobilizing muskoxen with etorphine, carfentanil citrate was obtained for testing since it is a more potent drug than etorphine and is supplied in concentrations of 3 mg/ml, thereby permitting utilization of much smaller-capacity syringe darts. Thirteen muskoxen were immobilized for radio collaring with the use of carfentanil, which appears to offer significant advantages over etorphine. A dose of 5 mg of carfentanil, 200 IU of lyophilized hyaluronidase, and 15 mg of acepromazine maleate were found to be effective for adult cows in the fall and for 3- to 5-year-old bulls in the spring. Four and one-half mg of carfentanil alone were not adequate for immobilizing an adult bull in the fall.

Reversal of the effects of etorphine was effected by injection of diprenorphine HCl (M50-50) at a ratio of 2 mg diprenorphine per milligram of etorphine. Half the dose of diprenorphine was administered intravenously via the external saphenous vein and half was introduced subcutaneously. Alternately, the full dose of diprenorphine was administered intramuscularly. The animals were able to rise in 2-15 minutes. Animals that were left undisturbed after antagonist injection generally took longer to stand than those that were encouraged to rise as soon as they were able.

Diprenorphine was also used to reverse the effects of carfentanil narcosis but naloxone dissolved in sterile normal saline solution at a concentration of 50 mg/ml was preferred.

Naloxone and diprenorphine both counter the effects of etorphine and carfentanil by competitive replacement at receptor sites. However, diprenorphine also produces respiratory and heart-rate depression similar to the agonist. Naloxone is a pure antagonist. Naloxone was used at a ratio of 100 mg naloxone per milligram carfentanil, half administered intramuscularly and half subcutaneously. Muskoxen sedated with carfentanil and reversed with naloxone were able to rise in 1-7 minutes. I suspect that naloxone/carfentanil ratios could be reduced and remain effective. The subcutaneous-intramuscular route of antagonist administration, rather than intraveneous injection, was used in later captures because naloxone is excreted much more rapidly than carfentanil, and recycling of narcotic through a hepato-enteric shunt or other pathway may result in renarcotization some time after reversal (Haigh 1982). It was assumed that uptake of naloxone would occur over an extended period when introduced into muscle and under the skin, to offset possible prolonged effects of carfentanil. Franzmann (pers. commun.) observed renarcotization of moose immobilized with carfentanil, and reversed with naloxone.

A large adult muskox bull immobilized 5 August 1985 near Nome, the first handled with carfentanil, was initially darted with 4.5 mg carfentanil. Two additional darts containing 3 mg carfentanil each were administered subsequently because the animal was still able to rise when approached and was extremely aggressive. The animal was eventually impaired enough to be physically restrained for marking. Forty mg of naloxone were administered intramuscularly and 40 mg were injected subcutaneously. The animal was up and able to run in 5 minutes. Fourteen hours after the initial darting the animal had moved 1.6 km from the capture location but was down again and did not rise when disturbed by an aircraft. Twenty-four hours post-capture the animal was able to rise but displayed poor control of its hindquarters. After 34 hours the animal had moved 4.8 km from the capture location but still appeared to be sluggish. No residual effects were noted after 48 hours. Following this episode both the initial dose of carfentanil and the dose of naloxone were increased and satisfactory performance was achieved.

My experience with chemical immobilization of muskoxen with the use of etorphine and xylazine, on Nunivak Island and in this study, indicates that muskoxen may have low tolerance for xylazine when it is used in combination with etorphine. Although it is not possible to isolate the cause of 4 delayed mortalities which occurred in pregnant cows captured 12 and 13 April 1984, I believe an overdose of xylazine may have been a contributing factor. One animal was double-darted with darts containing 7.5 mg etorphine and 35 mg xylazine and the other with 8.5 mg etorphine and 35 mg xylazine. Two of the animals died within 1.6 km of their capture location; 2 others were observed alive 4 days following capture but were found dead 14 days post-capture. One of the animals had given birth to a live calf. Necropsy revealed that uterine hemorrhage had occurred in the latter 2 animals. In light of these mortalities, and 2 similar occurrences in muskoxen handled in the Arctic National Wildlife Refuge (Reynolds et al. 1982), I believe drug capture of late-term pregnant females is inadvisable and that xylazine should be used in small doses. The possibility of antagonism of xylazine with yohimbine may offer increased latitude in using xylazine as a synergist.

Dart placement also appeared to be a factor in drug effectiveness. Darting in the hind leg as the animal faced away from the gunner was preferable to darting in the shoulder or in the lateral surface of the hind leg. During the fall I suspect that absorption of the drug in subcutaneous fat was responsible for incomplete anesthetization; this effect was countered by using 4.5-cm barbed needles and placing the dart lower in the hind leg to avoid areas of heavy fat deposition.

Use of a Herding Dog to Aid in the Capture of Muskoxen:

Recent methods for capturing large free-ranging mammals in North America have commonly relied upon pursuit with a helicopter to dart selected individuals. Although this method may be efficient in terms of time required to handle animals, it involves a number of intrinsic negative aspects for both the investigator and the animals.

Initial capture operations conducted on the Seward Peninsula utilized helicopter darting and the following disadvantages were noted:

1) The cost of using helicopters for captures was high.

2) Maneuvering helicopters close to the ground, particularly in high winds or in rising terrain in pursuit of an animal, is hazardous.

3) Muskoxen were difficult to dart from a helicopter. Their habit of turning to face danger, generally when the helicopter was in position for a shot, made it extremely difficult to place a dart in a favorable location, and extended pursuits were sometimes necessary.

4) It was difficult to select a specific individual from a herd that was being pursued at high speed.

5) Once an animal was darted it was difficult to follow in the tight group. If the animal did not

respond to the drug, subsequent darting was hampered by the problem of identifying the target animal.

6) Effective dart delivery was hindered by the need to shoot downward through a trailing skirt of guard hair. A significant number of darts missed completely or were deflected.

7) Social groups were broken up and cows separated from their calves. Jonkel (1975) also reported that animals darted from a helicopter could not be reunited with their herd. In small populations this impact could be substantial.

Harthoorn (1965) emphasized the problems associated with such stressful methods of capturing wild animals and indicated that in many cases methods could be used which would not subject animals to the violent, fear-producing episodes known to produce capture myopathy and other injuries.

Since earliest times, primitive hunters have used dogs to hold muskoxen stationary in their defense formation while they were killed (Gessain 1981). Historical accounts of muskox hunting methods employed by Indians and Eskimos in the North American Arctic and adopted by Caucasian explorers (Pike 1892; Whitney 1896; MacMillan 1918; Steffanson 1921, 1924; Hone 1934) described how hunters released several of their sled dogs to stimulate the formation of the group defense behavior to hold the muskoxen in place until the hunters methodically dispatched members of the group. Generally, they killed the entire herd. Early live-capture methods (Hone 1934) differed only in that once the adults had been killed the young were captured by hand or with lariats. Anderson (1966) reported on the use of sled dogs to hold herds in East Greenland during capture of calves; this is also the 1st reference to the use of dogs in drug-assisted muskox captures. Clausen et al. (1984) used sled dogs to hold herds when darting a large number of muskoxen in Greenland. The dogs were not trained for this work and were difficult to control. I first used a dog to hold muskoxen for chemical immobilization in 1984 near Nelson Island on the Yukon-Kuskokwim Delta. A Siberian husky was used to hold a herd of 12 muskoxen while 4 of the animals were drugged and marked. Although this dog was not trained for animal handling, the capture operation worked exceptionally well. Other dogs were used on the Seward Peninsula, including 2 Labrador retrievers and a border collie. Although untrained dogs were effective in eliciting the defense formation, they sometimes carried out too vigorous an attack and produced undesirable excitation in the muskoxen. Or, at the opposite extreme, the dogs lost interest after a short time and allowed the muskoxen to escape. In addition, these dogs were difficult to control when animals were immobilized.

In January 1986, I obtained an 18-month-old registered female Australian cattle dog. This dog performed admirably in testing and in actual capture operations. For example, 1 herd of 21 animals was held within a 25-m radius for 3 hours while the investigator moved openly to within 4 m of the herd (Figs. 1 and 2). Using this dog, one or more muskoxen from a herd could be darted at close range. Dart placement could be closely controlled and no darts missed their intended targets. Once the selected animals were down, the remainder of the herd was slowly moved away and held until the downed animals were marked, measurements taken, and specimens collected. The drugged animals were revived and allowed to rejoin the herd. Ideally, the animals did not run at all throughout the process, and if they did, it was for only a short distance.

The presence of a trained dog also greatly reduced potential hazards for personnel involved in the capture. If pressed closely, muskoxen will charge humans. My dog diverted these charges.

It is important when eliciting the defense formation for muskoxen to first become aware of humans or dogs from close range. If they observe the approach of the capture team from a distance they may stampede. Once this happens they may be difficult to stop. Large herds were particularly difficult to halt when they stampeded since the majority of animals were not aware that a dog was at their heels. Best results were obtained by using terrain features to block the investigators from the animals' view so we could approach within 100 m before releasing the dog. Once the herd was aware of the dog's proximity, capture personnel quickly followed up to reinforce the dog and provide additional stimulus to maintain the defense formation.

Growth of the Population, and Census Methods

None of the muskox populations established in Alaska were systematically censused in the initial phase of population growth and establishment. On the Seward Peninsula, incidental sightings and random aerial surveys carried out since 1970 and summarized by Grauvogel (1984) provide a general picture of population growth. The 1980 count was considered the best estimate of population size prior to the current study. However, Grauvogel (1981) reports that this figure was derived by combining a March 1980 count of 51 animals in the "Nuluk Herd"; the observation of 10 calves in May; and a count, obtained in June of 43 animals in the "Black Mountain Herd." For this exercise to be valid, one must assume greater herd cohesion and home range fidelity than observed in other muskox populations (Gray 1973, Smith 1976, Reynolds et al. 1985) and that muskoxen on the Seward Peninsula behaved differently in

Fig. 1. Plastic streamers attached to the horns were highly visible from the air but were not retained long enough to be useful as a marking method.

Fig. 2. Red cattle ear tags proved to be the most effective method for marking muskoxen for field identification.

Fig. 3. A group of muskoxen could be held indefinitely in the defense formation by a trained Australian cattle dog.

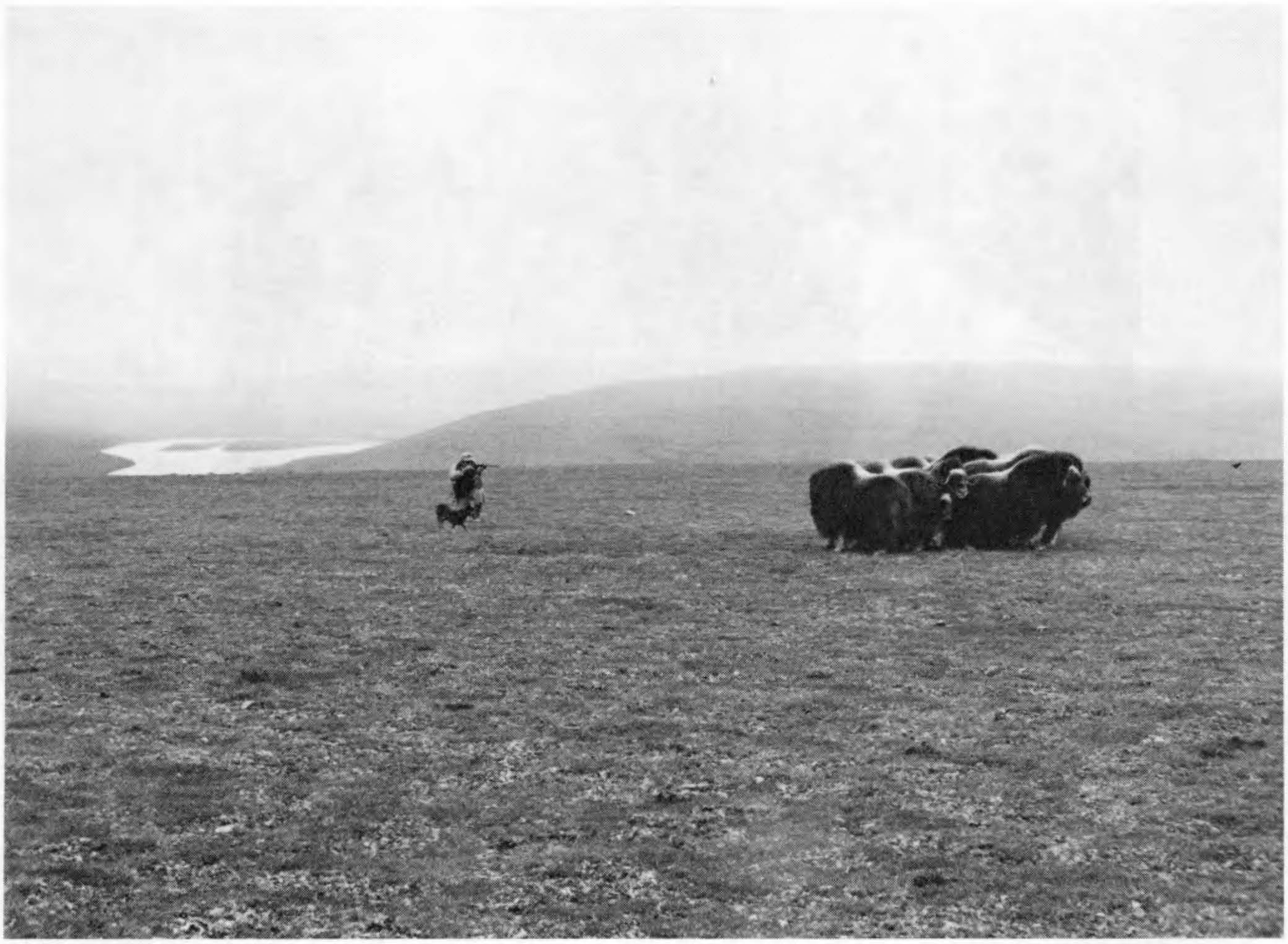

Fig. 4. Muskoxen were darted at close range when held in the defense formation by a herding dog.

Fig. 5. Once an animal was down the rest of the herd was moved a short distance away and held until the anesthetized animal was revived and allowed to rejoin the group.

1980 than they do today. One must also accept Grauvogel's (1978, 1979, 1980, 1981, 1984, unpubl. data [ADF&G, Nome]) contention that the animals sighted in areas not considered the range of the Nuluk or Black Mountain herds were lost from the population.

Muskoxen occur on the Seward Peninsula at low densities in widely dispersed groups. Previously, counts were conducted by aerial visual search using irregular transects. Because different portions of the range were covered at different times, movements of groups among areas and between survey periods may have resulted in erroneous population estimates. Because of the clumped distribution of the population, missing 1 or more groups could also have resulted in large errors in the population estimates. These errors would have been particularly significant for a small population.

Search intensity sufficient to ensure that all groups were located was prohibitive in terms of the required flight time. A sample of radio-collared animals, well-distributed within the population, was proposed as a means of reducing the required flight time without increasing the possibility of missing groups. Radio-collared animals have been available in the Seward Peninsula muskox population since 1981. The number of collared animals was increased in 1983 to an estimated 4% of the population (Table 5). The potential movement of animals between "herds" was not fully recognized in 1983. We combined ground composition counts from the south side of the Seward Peninsula in October, with ground composition counts of groups located with the aid of radiotelemetry the following April; the combination resulted in a total of 162 animals. A subsequent count in 1984 indicated a 38% increase between 1983 and 1984, which is higher than has been reported in the literature; the percentage is also higher than observed rates of calf production on the Seward Peninsula. Apparently the 1983 census underestimated the population by at least 10-15 animals. Nonetheless, this exercise demonstrated the value of radiotelemetry in censusing muskox populations; subsequent censuses (1984 and 1985) using higher proportions of instrumented animals obtained results which I felt closely approximated actual population size.

If the herds which included the 16 radio-collared animals were the only groups counted, no more than 55 animals would have been missed in the 1985 census, assuming radio-collared animals were randomly distributed in the population. However, considerable effort was expended to further increase the accuracy of the estimate by visually locating herds that contained no radio-collared individuals.

Survey conditions in 1985 were ideal, with complete snow cover, restricted range availability due to deep snow, and

Table 5. Active radio collars, estimated population size, and percent radio-collared animals at time of April census, 1983-85.

Year	Active radios	Population census	% Radio-collared animals
1983	7	175[a]	4
1984	14	225	6
1985	16	271	6

[a] Corrected for animals missed. See text.

unlimited visibility. One muskox herd was sighted from 8,500 feet above ground level and it is unlikely that any large bands were missed within the area covered.

By March 1986, the percentage of muskoxen with operating radios had declined from 6% to 3%. Although 6 additional animals were radio-collared during March and April 1986, they did not have sufficient time to become distributed in the population and a meaningful census was not possible.

One group of muskoxen on the Seward Peninsula contained 71 animals. Groups frequently included 50-60. Counting these large groups from the air is not feasible and errors in visually counting large groups may have been significant in muskox censuses conducted in other areas (T. Smith, unpubl. data). I first used black and white prints made from 35 mm negatives to census muskoxen on Nunivak Island in 1979 and on Nelson Island in 1980. In the present study, herds located in 1984 and 1985 were photographed from the air using 35 mm color transparencies (Fig. 6).

Photographs were taken from a Cessna 185 equipped for radio-tracking. The photographer sat behind the pilot and took a series of exposures using a 35 mm camera with a 70-210 mm zoom lens and a motor drive as the aircraft circled the herd at 500 feet above ground level. Substantial experience with this method on the Seward Peninsula, Nunivak Island, and Nelson Island has convinced me that this is the only way to obtain accurate counts of large muskox herds. By comparing frames it was possible to determine the actual number of individuals in a herd. Photo counts differed by as much as 25% from visual counts made by observers. This disparity was inversely proportional to the size of the herd and the experience of the observer. Photographs were most readable when taken against a snow-covered background when the sun was high and skies clear. Conditions conducive to this type of census on the Seward Peninsula occur in April.

The costs of muskox census methods were discussed by Smith et al. (1986) and it was concluded that for any level of required accuracy, a photocensus aided by radiotelemetry will be the least costly means of enumerating the population.

Movements

It has been reported by a number of authors that muskoxen are sedentary and faithful to a fixed home range (Pedersen 1958, Miller and Gunn 1980, Jingfors 1980, Vincent and Gunn 1981). Wilkinson (1971:689) commented on "the naturally sedentary nature of muskoxen." Some muskoxen on the Seward Peninsula fit this description; 1 female transplanted from Nunivak

Fig. 6. The number of animals in groups photographed from the air could be readily determined.

Island occupied an area within a 9.3-km radius from 28 November 1981 to 27 January 1987. At the other extreme, a male observed for 30 months was located at points 172 km distant from each other (Table 6). This animal moved a minimum of 132 km in 2 months. Twenty muskoxen that were followed in this study, for which at least 12 months of data are available, ranged over larger distances than 37 radio-collared moose (20 females, 17 males) studied on the Seward Peninsula during the years 1981-85 (Fig. 7). These values are the maximum distance measured across all points accumulated for an individual animal, or the minimum width of its home range. Maximum distance between observations for individual muskoxen averaged 84 km; for moose the mean was 50 km.

More rigorous analysis of movement data will require digitization of locations and will be presented in a future report.

Social Dynamics

Muskoxen are highly gregarious and any discussion of ecological relationships must take into account the group dynamics of the population.

Pegau (1973) named a group of 21 muskoxen transplanted in 1970 near the Nuluk river, the "Nuluk Herd." Additionally, Grauvogel (unpubl. data [ADF&G, Nome]) proposed that a new herd (named the "Black Mountain Herd") occupied an area in the vicinity of Black Mountain (Fig. 8). Subsequent reports (Grauvogel 1978, 1979, 1980, 1981, 1984) expanded the hypothesis that the Seward Peninsula muskox population occurred as 2 discrete herds. The term "herd" as used by the above authors was never clearly defined, but apparently the expectation was for these herds to grow as independent cohesive units in a manner normally ascribed to populations. Grauvogel (1984) elaborated the Nuluk/Black Mountain herd concept and presented available population data according to that pattern even though considerable evidence indicated that the 2 nebulous herds were neither cohesive nor discrete (Figs. 5-8). Interestingly, the Nuluk Herd disbanded in April 1972, less than a year after its creation, and was not seen as a unit throughout the year (Pegau 1974).

The record of muskox sightings (Figs. 9-12) in locations far removed from the designated ranges of the 2 herds in early years were thought to represent animals destined for mortality. Grauvogel (1980) maintained that, "Since a number of strays were sighted considerable distances from the nearest known muskox herd, it is not likely that very many (if any) ever returned. Animals that wander away from the nucleus herd during the summer foraging period probably contribute significantly to herd attrition." Other reports (Grauvogel 1978,

Table 6. Maximum distance between cumulative locations for individual radio-collared muskoxen on the Seward Peninsula, 1981-86.

Sex	Maximum distance between observations (km)	Months active
F	139	69
F	19	69
F	143	21
F	50	22
F	26	37
M	102	15
M	70	21
F	41	19
F	24	55
M	97	22
F	111	51
F	26	37
M	39	30
F	31	53
M	143	12
F	30	10
F	133	37
F	101	16
M	87	35
M	173	30
M	33	8
M	83	6
M	112	17
M	86	9
M	33	10
M	33	9

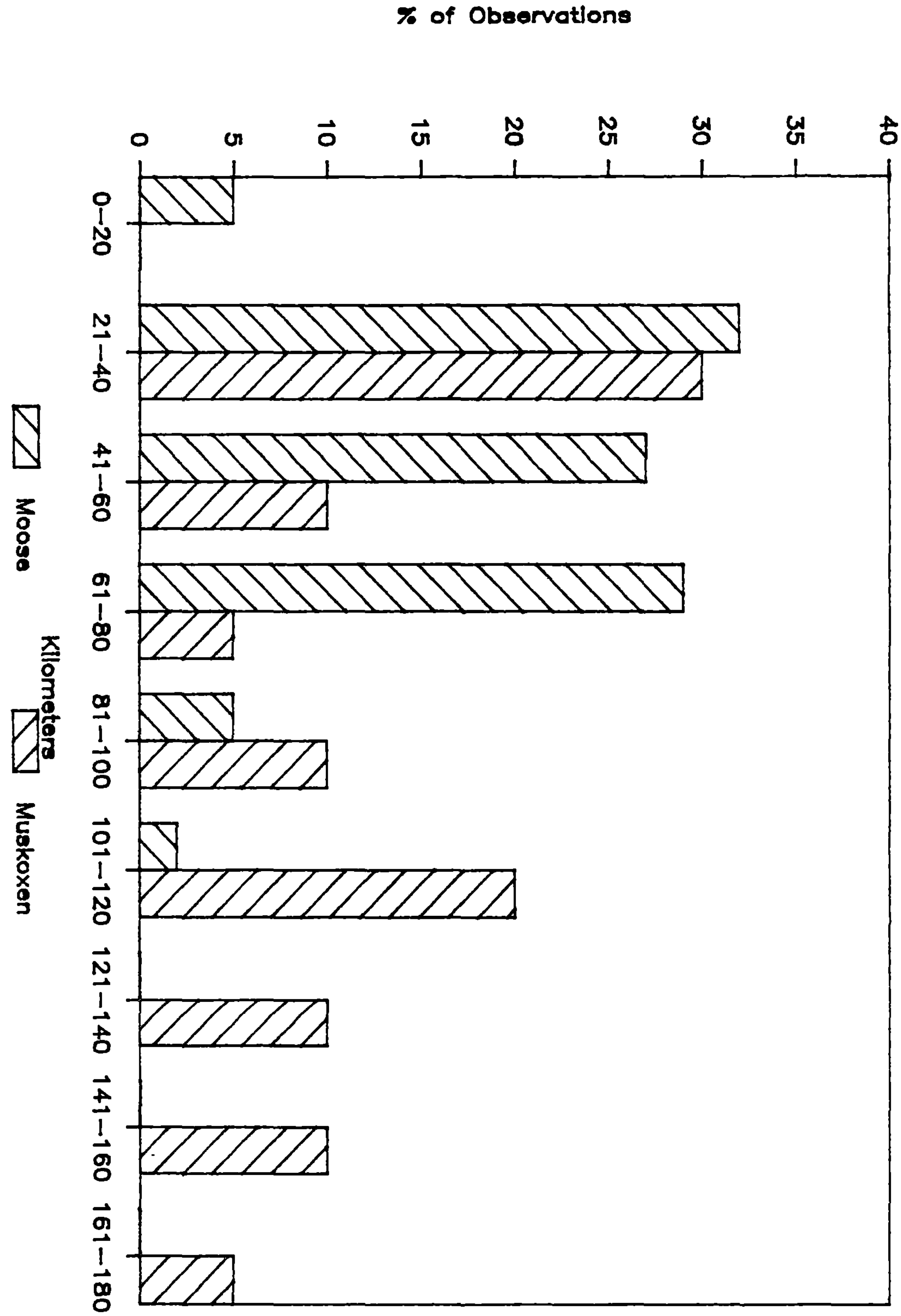

Fig. 7. Maximum distance measured across all location points for individual radio-collared muskoxen and moose on the Seward Peninsula, Alaska 1981-1987.

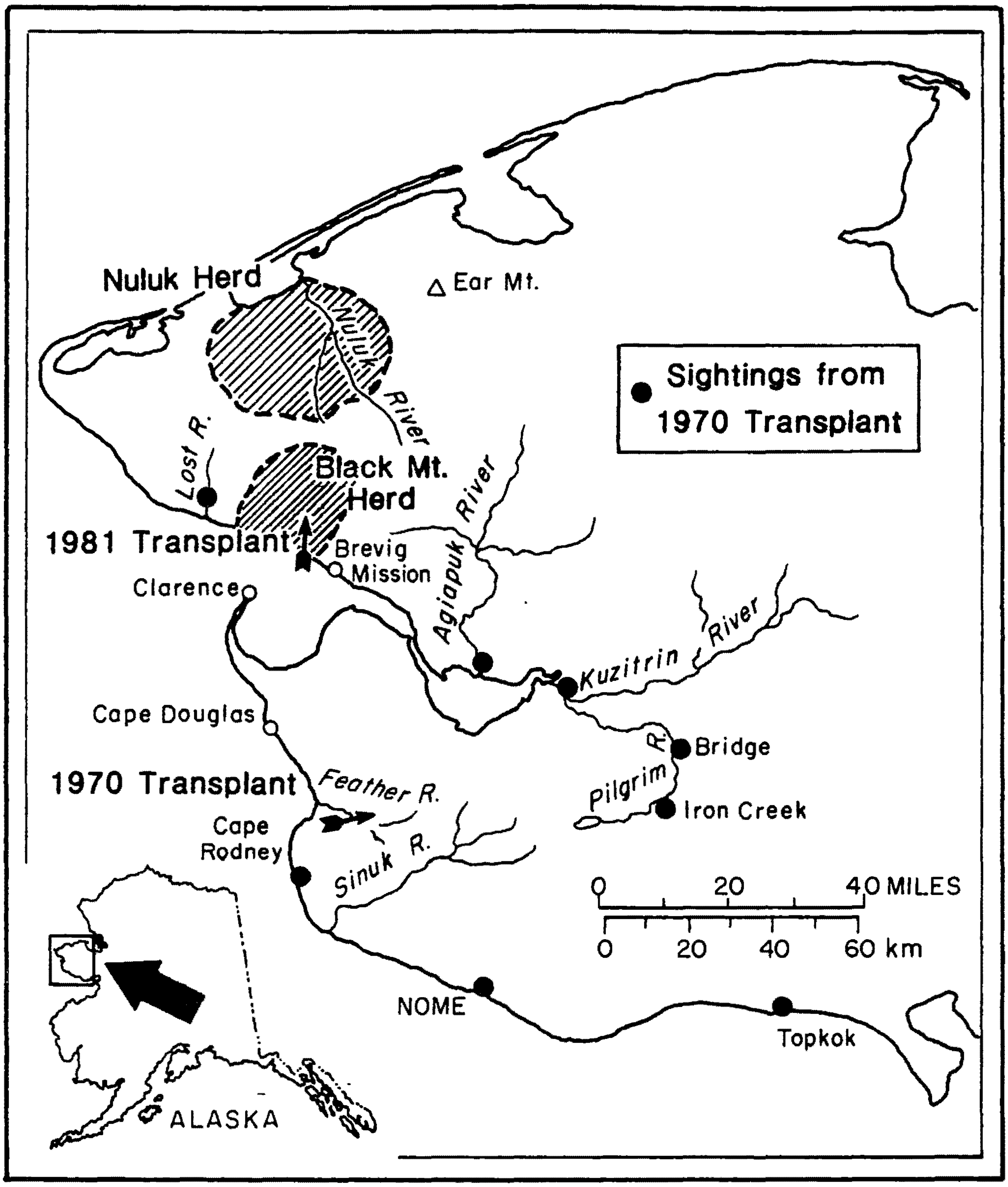

Fig. 8. Release sites for muskoxen transplanted to the Seward Peninsula in 1970 and 1981 and the range of the Nuluk and Black Mountain herds proposed by Grauvogel (1984).

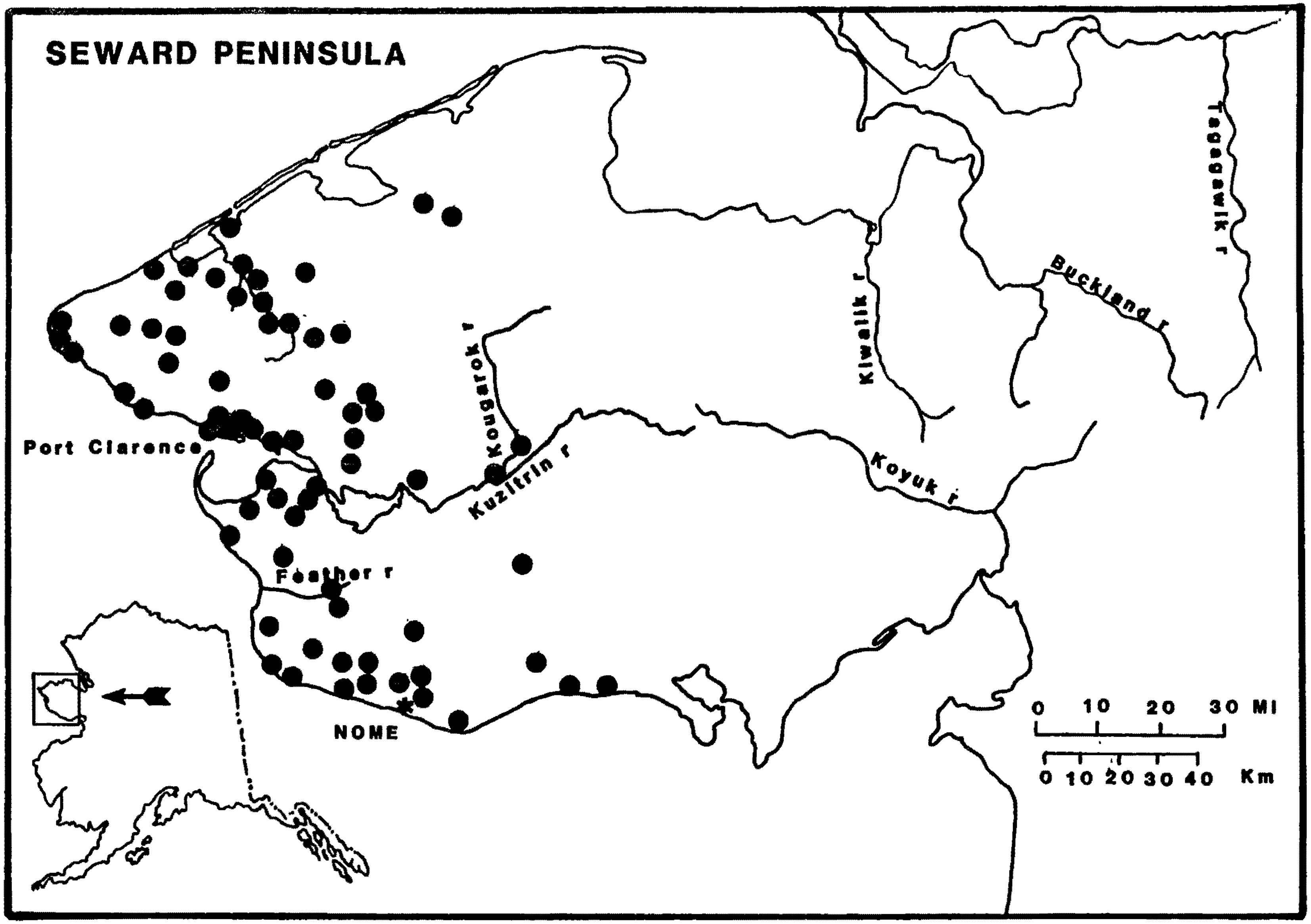

Fig. 9. Sightings of muskoxen on the Seward Peninsula reported by the public, 1970-74.

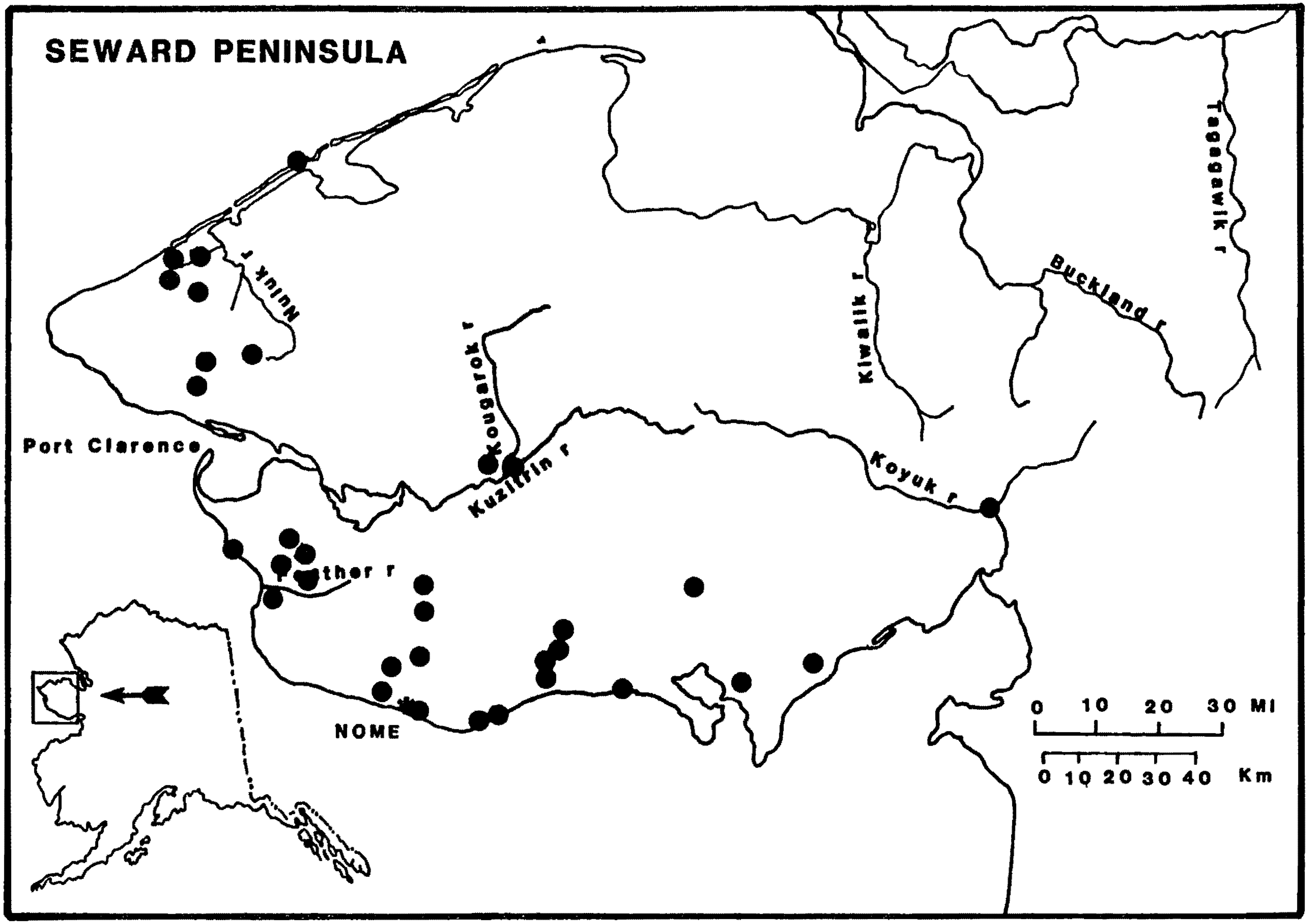

Fig. 10. Sightings of muskoxen on the Seward Peninsula reported by the public, 1975, 1976, 1979.

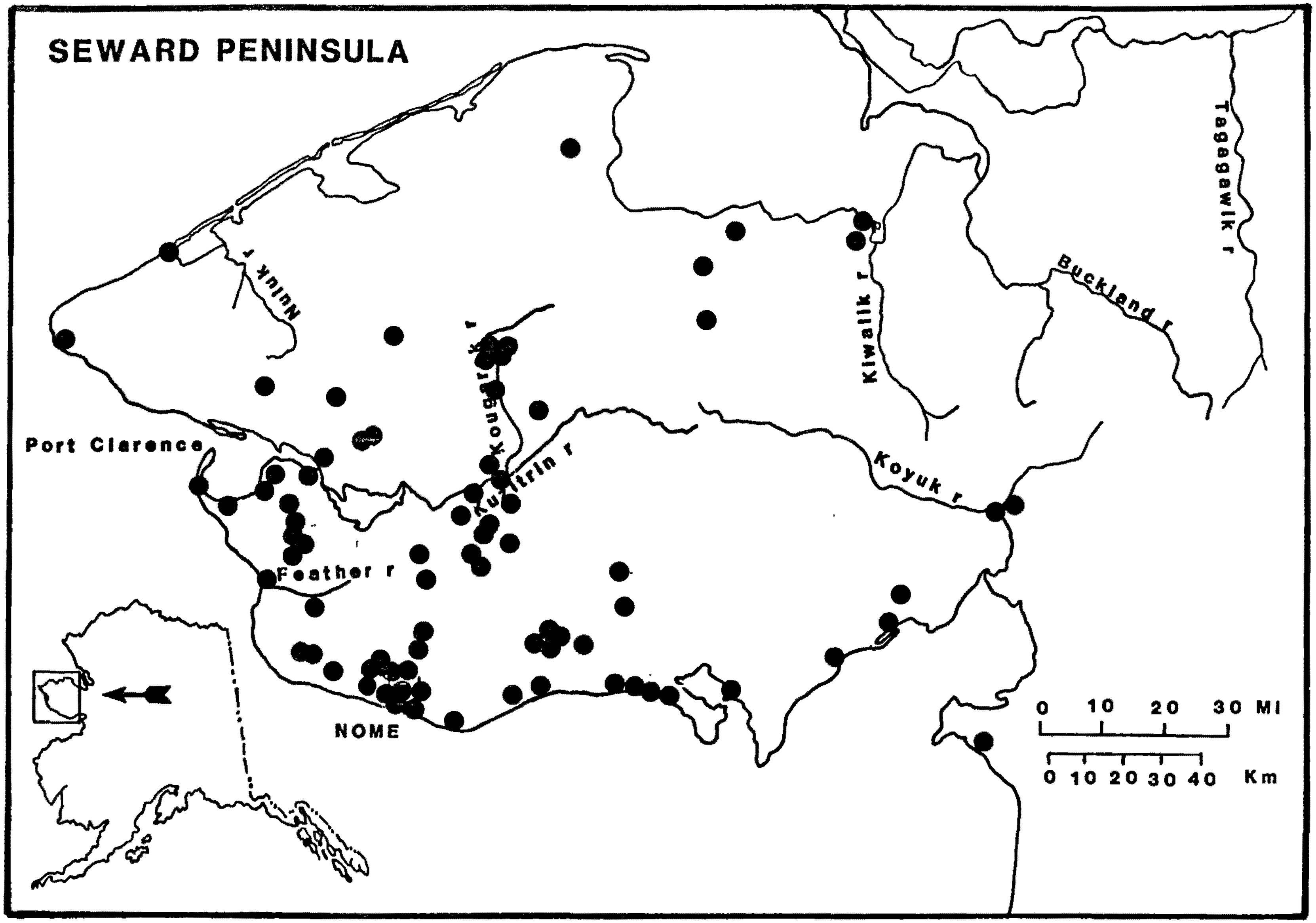

Fig. 11. Sightings of muskoxen on the Seward Peninsula, reported by the public 1980-84.

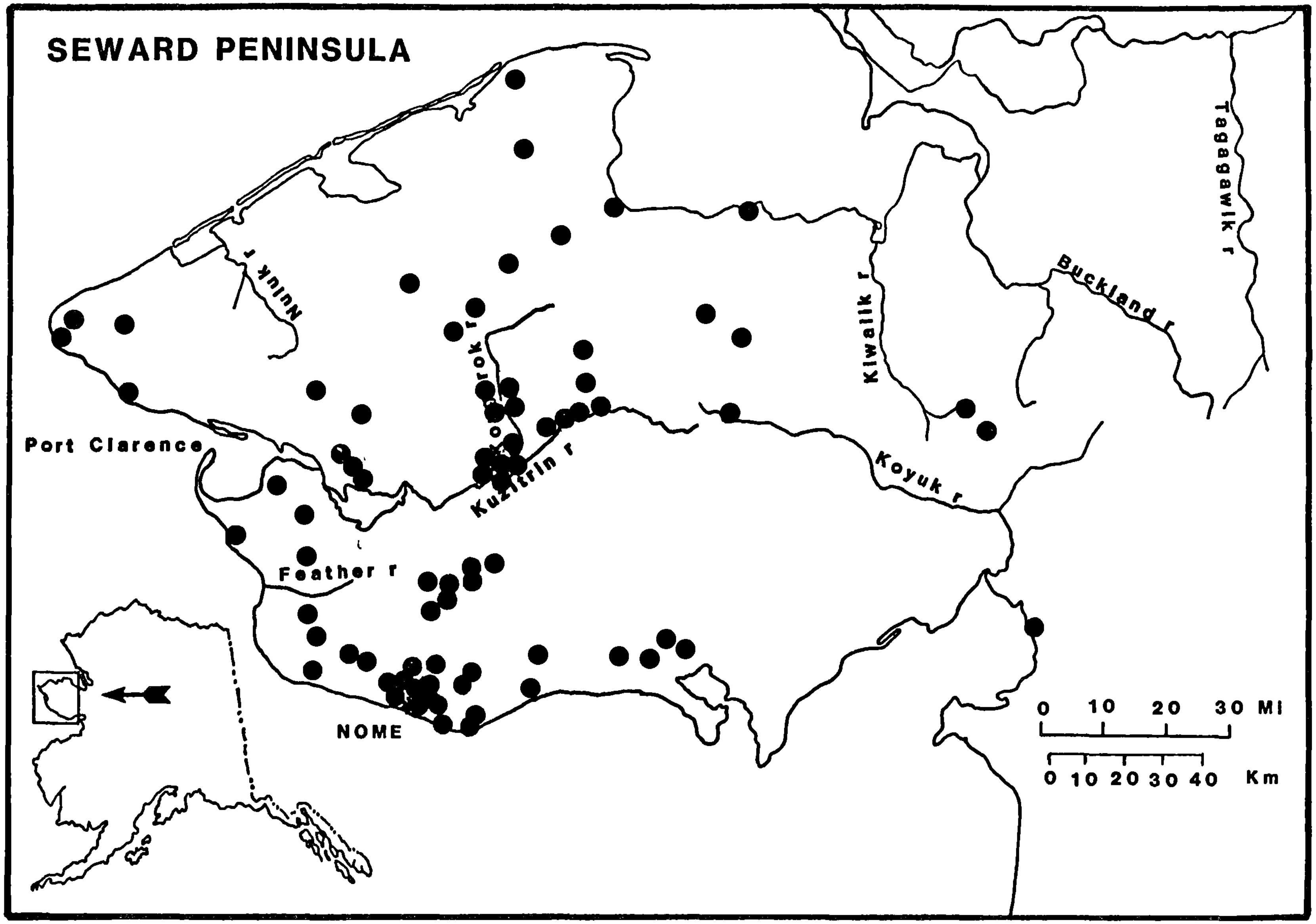

Fig. 12. Sightings of muskoxen on the Seward Peninsula, reported by the public 1985-86.

1980, 1984, unpubl. data [ADF&G, Nome]; Nelson 1982) echo the conclusion that movement away from the main herd is paramount to annihilation. Direct observations supporting this concept are limited (Appendix B).

Twelve of 20 radio-collared muskoxen that were followed in the present study and assigned a herd affiliation based on capture location, eventually moved out of the designated range of their herd. Five of 20 animals moved between the designated ranges of the 2 herds. Two of 8 animals collared outside the ranges of the 2 herds moved into 1 of the designated ranges and joined with resident animals in the area. The other 6 animals collared at distant locations have accumulated only 9 months (2 animals), 10 months (3 animals), and 17 months (1 animal) of observations and may yet enter an established herd.

There is little evidence that traveling to remote locations is more hazardous than remaining within one of the designated ranges. Five mortalities of radio-collared animals were observed. Only 1 of these occurred outside the ranges of the Nuluk or Black Mountain Herds. Ironically, 1 bull collared on the Kougarok River moved 82 km into the safety of the designated range of the Black Mountain Herd, acquired a harem, and died.

Previous authors credited muskoxen with little ability to navigate. Observations of radio-collared animals on the Seward Peninsula do not support this view. For example, a collared female moved 131 km from the center of the Black Mountain Herd range and returned within 3 months.

Associations between individuals are perhaps more important, with regard to population biology, than fidelity to a geographical area. Animals within a herd should be expected to associate with conspecifics within the herd and not with members of another herd. Each time a radio-collared muskox was located in a group with another instrumented animal, the association was recorded (Table 7). Herd assignments are based on the geographic location where the animal was captured (Table 8).

Table 7 shows that about one-fourth of the associations do not fit the pattern which would be expected if the herds were isolated. Clearly, animals from the Nuluk Herd commonly associate with animals that do not remain within either of the designated ranges. The small numbers of observed associations between animals from the Nuluk Herd and the Black Mountain Herd (<2%) may result from the paucity of instrumented animals assigned to the Black Mountain Herd and the consequent low probability of detecting associations.

Table 7. Number of associations observed between radio-collared muskoxen classified as members of the Nuluk Herd, the Black Mountain Herd, or as unclassifiable.

Herd	Number of observations
Blk-Blk[a]	4
Blk-N[b]	2
N-N	81
N-U[c]	32
U-U	31

[a] Blk = Black Mountain Herd.
[b] N = Nuluk Herd.
[c] U = Unclassifiable.

Table 8. Number of radio-collared muskoxen classified as members of the Nuluk Herd, the Black Mountain Herd, or as unclassifiable, based on capture location.

	Nuluk	Black Mountain	Unclassifiable
	14	3	10
Percent	51.8	11.1	37.0

Knowledge gained from study of the movements of marked animals provides a basis for interpretation of the public sighting record. Sightings by the public have provided a valuable source of information to document the distribution of muskoxen on the Seward Peninsula (Figs. 9-12). For this analysis, 214 sightings of muskoxen outside the range of the Nuluk and Black Mountain Herds during the years 1970-1986 were tabulated. Of these, 171 (80%) were made during July to October. One hundred twenty, (56%) were made in August and September. Of 22 sightings for which sex and age information is available, 18 were of adult bulls.

Group Size

The Black Mountain and Nuluk herds certainly did not grow as cohesive units. The mean sizes of groups of muskoxen which included at least one radio-collared individual are shown by month for combined data from 1981-86 (Table 10) (Fig. 13). Changes in mean herd size are typical of muskox populations studied in other areas (Tener 1965, Gray 1973, Reynolds et al. 1985). Herds are larger in winter than during the rut (Aug-Sep) when competition between bulls is most intense.

Population Regulators

The Seward Peninsula muskox population can be expected to grow and expand its range throughout the foreseeable future. There is no reason to suspect that habitat quality or availability will become limiting in this century. Observed mortality has been low (Appendix B). Predators are not known to have had an impact on the population. Wolves are extremely rare on the Seward Peninsula. Brown bears are common but predation on muskoxen is apparently a rare occurrence. Only 1 well documented description of brown bear predation on muskoxen is reported in the literature (Gunn and Miller 1982); however, a number of observations of bears feeding on carcasses have led others to speculate that bears may have killed the animals rather than having scavenged animals that died from other causes (reviewed in Gunn and Miller 1982, Reynolds et al. 1985).

A very old male muskox captured on the Seward Peninsula in April bore partially healed parallel scars on 1 shoulder and had a patch of hair torn from the back near the saddle (Fig. 14). It did not appear that these wounds could have been inflicted by another bull in a rutting battle. It is possible that either a wolf or a bear could have made such injuries with its teeth or claws.

The almost complete absence of records of predation on muskoxen by brown or polar bears--particularly their absence from

Table 9. Mean herd size and number of herds containing at least 1 radio collared muskox 1981-86.

Month	Mean herd size	Range	n
Jan	13.0	1-51	23
Feb	13.0	3-40	10
Mar	16.6	2-65	11
Apr	15.3	1-71	42
May	8.7	1-30	38
Jun	9.2	1-47	35
Jul	9.8	1-30	18
Aug	7.5	1-26	39
Sep	9.4	1-51	29
Oct	11.5	1-35	39
Nov	12.7	1-48	21
Dec	12.8	1-55	26

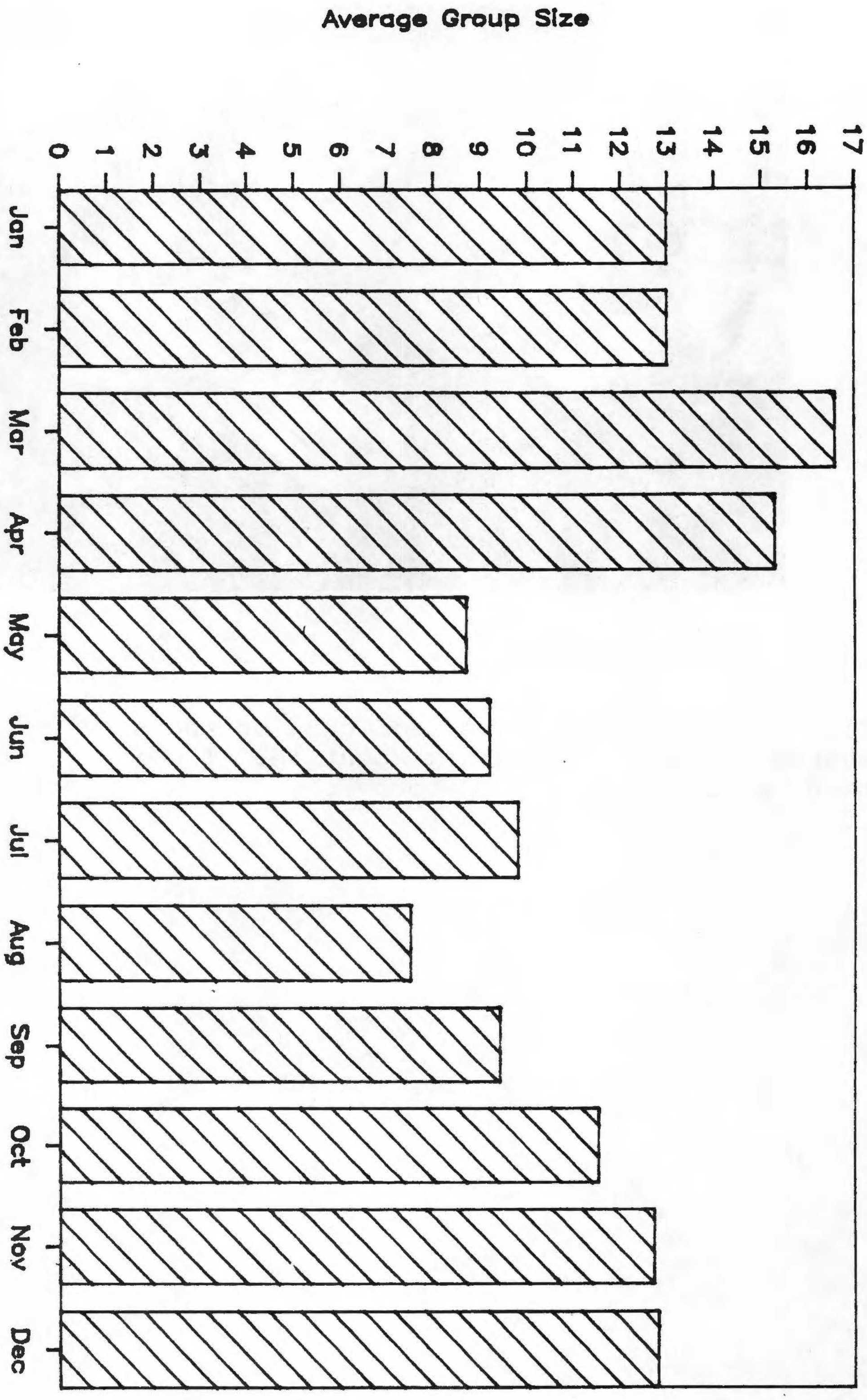

Fig. 13. Mean group size by month for muskox groups which included at least one radio-collared animal, Seward Peninsula, Alaska 1981-1986.

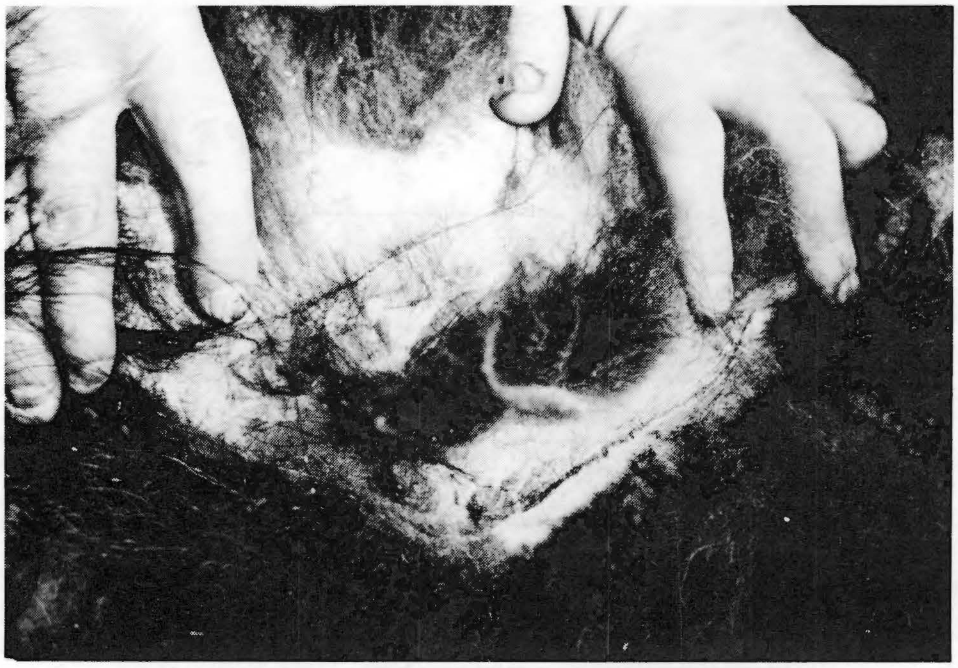

Fig. 14. A partially healed wound on the shoulder of a bull muskox captured near Black Mountain. The injury could have been inflicted by a predator.

the accounts of the early Arctic explorers (Steffanson 1924)--seems to indicate that these predators do not utilize muskoxen as a common prey species. However, the importance of some forms of predation, and in particular that which occurs on neonates of other species (e.g., moose) was only recognized recently and cannot be ruled out as a population regulator. There is also evidence that learning is important in bears' prey selection (W. Ballard, pers. commun.); a longer association between the species may give rise to bears that specialize in muskox predation. The observation of a radio-collared bear feeding on 2 separate muskox carcasses in the Arctic National Wildlife Refuge (P. Reynolds, pers. commun.) may demonstrate bears may have learned to prey on muskoxen in that area.

Muskoxen in the wild are remarkably disease- and parasite free. Serum samples from 12 animals were screened for the presence of antibodies for contagious ecthyma, epizootic hemorrhagic disease, bluetongue, bovine viral diarrhea, infectious bovine rhinotracheitis, parainfluenza III, brucellosis, leptospirosis, and Q fever. One low-level positive titer for contagious ecthyma and 2 low-level positive titers for leptospirosis was measured. No overt pathological manifestation of these diseases was noted in the animals which tested positive. The lack of evidence of exposure to Brucella suis is particularly significant since muskoxen on the Seward Peninsula are exposed to reindeer herds in which brucellosis is endemic. A muskox from the barren lands of Canada was determined to be infected with rangiferine brucellosis (Gates et al. 1984) which demonstrates that muskoxen are susceptible to the disease.

Data on calf production were obtained from aerial surveys. In July 1985, 21 calves were observed in a sample of 96 muskoxen (22%). Two surveys conducted on 15-29 May and 30 June 1986 recorded 16 calves in a sample of 84 animals (19%) and 17 calves among 119 muskoxen (14%), respectively.

Calving on the Seward Peninsula occurred primarily in May, (Table 10). The earliest that a calf was observed on the Seward Peninsula was 29 April. Alendal (1971) added a review of existing records to his own observations to determine a gestation period of 35-36 weeks. Based on this period, 1st breeding of muskoxen on the Seward Peninsula took place in the latter part of August. Muskoxen do not exhibit a closely synchronized calving period as recorded for caribou. I observed a newborn calf on 20 June 1973, on Nunivak Island; this suggests that the conception period must extend from mid-August to the 1st part of October.

Table 10. Dates of 1st muskox calf production on the Seward Peninsula, Alaska, 1982-86.

Date of survey	Observation of calves	Total muskoxen observed
22 April 1982	0	--
29 April 1982	2	--
29 April 1982	5	--
26 April 1983	0	--
27 April 1983	0	--
27 April 1984	0	10
03 May 1984	3	13
03 May 1984	2	150
23 April 1985	0	12
26 April 1985	0	12
30 April 1985	1	13
02 May 1985	1	13
10 May 1985	1	13
12 May 1985	2	14
19 May 1985	2	14
21 May 1985	3	15
13 May 1986	0	12
15 May 1986	3	15

Hematologic parameters from muskoxen immobilized with drugs during the course of this study are shown in Appendix C. Small sample sizes and the paucity of baseline values for free-ranging muskoxen do not allow interpretation of these data and they are presented for reference.

Conclusions

When Congress authorized the expenditure of funds to reestablish muskoxen as a native species in Alaska, it was recognized that the undertaking would be a long one. Given the decline in availability of funds for further transplants, the established populations acquire inordinate importance. Repopulation of habitat in Alaska probably could occur through expansion and radiation from existing populations because data obtained in this study, as well as in the Arctic National Wildlife Refuge, indicate a slow but steady expansion in numbers and distribution. The 2 other populations which could contribute to repopulation of unoccupied range do not appear likely to play an important role. The Cape Thompson population derived from transplants in 1970 and 1977 has shown very little increase. The Nelson Island population is currently harvested near replacement level. Hence, it is essential that the 2 populations (Fig. 15), which can provide animals to repopulate the vast areas of suitable habitat, be protected and properly managed. If no further transplants are conducted, the time required to reach carrying capacity will be long, perhaps a century. A unique opportunity exists in enhancing muskox populations in Alaska and elsewhere in that muskoxen have been brought back from the brink of extinction to a habitat that is virtually intact. By spring 1986, Alaskan muskox populations totaled at least 1,700 animals. I have no doubt that with effective management, Alaska could support 10 times that many.

Past attempts to predict carrying capacity of a habitat for muskoxen have only demonstrated the inadequacy of those estimates. The carrying capacity of Nunivak Island was estimated at various times to be 300 (Lent 1974), 500 (Spencer and Lensink 1970), 2,100 (Palmer and Rouse 1945), 5,000 (Palmer 1938) and 5,830 (Bos 1967). It was recommended that the Nelson Island population be limited to 75-100 animals (Griffin 1976). At least 287 muskoxen were there in spring 1986, with no indication that the range was overpopulated. To speculate on the optimum population for the entire State would be meaningless at this point. However, it appears that previous characterizations of habitat requirements for muskoxen were overly conservative and that the species is much more adapatable than was formerly thought. Potential habitat appears to be extremely abundant and widespread. On the Northern Seward Peninsula, muskoxen will soon outnumber moose.

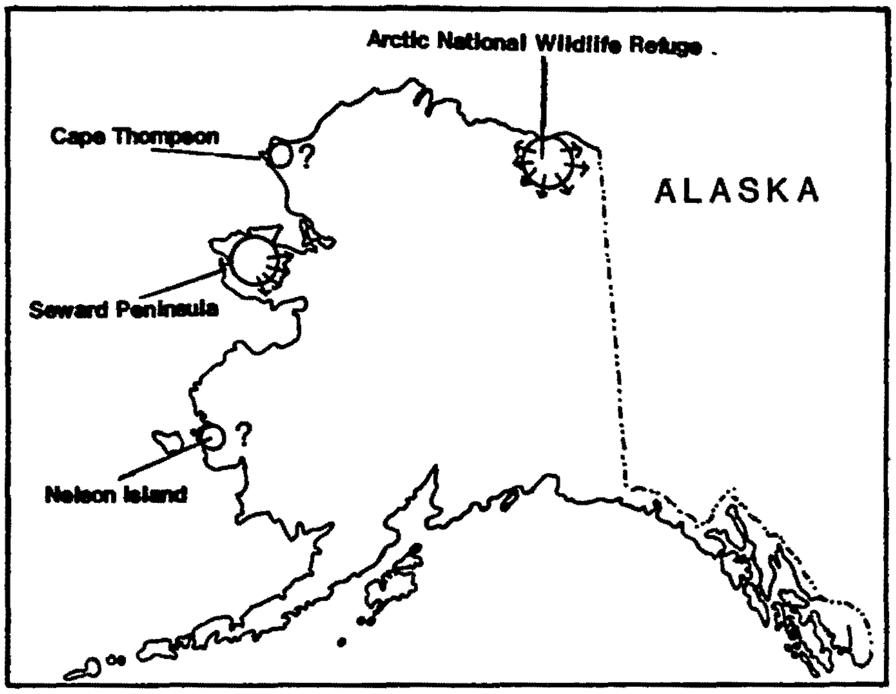

Fig. 15. Locations of muskox populations which could repopulate Alaska through range expansion.

Tener (1965) compared productivity of muskox populations in the high Arctic to that of deer populations in temperate climes and concluded that muskoxen would never be of significant economic importance because their intrinsic productivity was too low. Experimental evidence has shown that Tener was incorrect in his assumption that muskoxen are obligate specialists in arctic desert ecosystems. Muskox populations that he exemplified as stereotypic, in the extreme arctic, were more likely relict and living in marginal habitat for any herbivore. On Nunivak Island, from 1975 through 1986, 595 muskoxen were killed by hunters and 162 were removed in live-capture operations. The population remained stable at around 500-600 animals. Hunters have removed about 15% of the Nelson Island muskox population annually since 1981 and the population has grown. Obviously, not all muskox populations are as unproductive as Tener (1965) predicted and utilization of muskoxen on Nunivak and Nelson Islands has brought substantial economic benefit to the state.

Competition with the other widely distributed tundra herbivore, caribou, does not appear likely at this point. Only 1 example of deleterious competition between the species has been observed. Klein (1984) described how competition between reindeer and muskoxen on Svalbard resulted in the extinction of the muskox population. However, this island situation is unique and not necessarily pertinent to the question of potential competition elsewhere. Reindeer and muskoxen have coexisted on Nunivak Island for more than 50 years without significant overlap. Intuitively, it seems the competitive exclusion principle would demand that since Rangifer and Ovibos evolved together for hundreds of thousands of years, they must have developed strategies to partition the range or 1 species would have perished. It is axiomatic that a diverse herbivore fauna can utilize forage resources more efficiently than a simple one. Even if some niche overlap occurs at high densities, 2 species should be able to produce higher herbivore biomass and ecosystem stability than either one alone.

Popular articles and some professional game managers have argued that since muskoxen are polygynous, only a few bulls are required to maintain a healthy population. They assumed the mobile, lone bulls or bull groups observed during the rut to be as wasted animals, doomed to live in isolation or to die of unknown causes. Smith (1976) and Alendal (1983) questioned this view, which had never been supported with empirical evidence. The information derived in this study has shown a much different picture of those movements and provides a basis for a new hypothesis concerning the role of bulls in an expanding population. I suggest that pioneering of winter habitats by bulls is an important adaptation for utilizing discontinuous habitat and that this is the primary mechanism by which muskoxen colonize new areas.

Muskoxen demonstrate an uncanny ability to locate each other, which is probably an adaptation to living in low-density, widely dispersed groups. Regular influx and dispersal of animals occurred in a group which included a radio-collared cow whose range from 1981 through 1987 could be encompassed by a 9.3-km radius in a location far removed from other areas commonly used by muskoxen. Throughout the study, no bulls that were collared alone, and no collared bulls that separated from a group remained alone.

Findings in the current study do not indicate the existence of persistent, identifiable groups within the Seward Peninsula muskox population. Historical data do not permit a meaningful evaluation of the hypothesis that isolated herds once occurred. Some separation of movement patterns coinciding with the continental divide on the western portion of the Seward Peninsula were noted, but movements across this line occur and I conclude that the Seward Peninsula muskox population is homogeneous.

ACKNOWLEDGMENTS

This work was funded by Federal Aid in Wildlife Restoration, the U. S. Bureau of Land Management, and the National Park Service.

John Knudsen, Bob Nelson, Scott Robinson, Scott Schliebe, Rita Smith, Carl Grauvogel, Dave Anderson, Eric Pentilla, and David Blair assisted at various times in capture operations. Bob Nelson, Carl Grauvogel, Charlie Lean, and Dave Anderson participated in relocation flights. Dave Anderson and Carl Grauvogel provided editorial comments on the 1985 and 1986 progress reports. Steve Machida, Steve Peterson, and Barbara Townsend reviewed this report, and Idell Parkhurst provided invaluable assistance in typing and organizing drafts of the manuscript.

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Appendix A. Identification and status of marked and radio-collared animals on the Seward Peninsula, 1981-86.

Animal/ visual collar number	Sex	Date collared	Location	Approximate age at collaring (years)	Plastic ear tag Nos. & color		Metal ear tag nos.		Horn streamer colors		Radio status, Jan 1987
					Left	Right	Left	Right	Left	Right	
1/45	F	3/24/81	Pt. Clarence	4+	--	--	334[a]		--	--	Functional
2/--	M	10/18/83	Pinguk R.	0.5	R20	R20	--	--	--	--	Not collared
3/46	F	3/25/81	Pt. Clarence	2+	--	--	369[a]		--	--	Animal dead, fall 82
6/47	F	3/24/81	Pt. Clarence	3+	--	--	13[a]		--	--	Animal dead, fall 82
8/48	F	3/24/81	Pt. Clarence	3+	--	--	29[a]		--	--	Functional
11/--	M	10/18/83	Nuluk R.	6-7	R2	R2	--	--	Or	Or	Last located 07/17/85
12/43	F	6/23/82	California R.	13	R66	R66	10035	10036	--	--	Animal dead, 4/09/84
13/--	F	10/18/83	Upper Nuluk	5-6	R3	R3	--	--	Wh	Wh	Functional
14/--	M	4/12/84	Pinguk R.	6+	R4	R4	17224	17225	Red	Wh	Functional
15/--	M	10/18/83	Pinguk R.	6-7	R5	R5	--	--	Red	Red	Last located 07/17/85
16/64	F	6/23/82	Pinguk R.	3	R64	R64	17207	17208	--	--	Last located 1/25/84

Appendix A. Continued.

Animal/ visual collar number	Sex	Date collared	Location	Approximate age at collaring (years)	Plastic ear tag Nos. & color		Metal ear tag nos.		Horn streamer colors		Radio status, Jan 1987
					Left	Right	Left	Right	Left	Right	
18/61	F	6/23/82	Nuluk R.	3	R68	R68	17204	17203	--	--	Functional
19/--	M	4/12/84	Nuluk R.	8-10	R7	R7	17236	17235	Blk	Red	Last located 02/18/86
20/63	F	6/23/82	Cooper Cr.	--	R63	R63	17205	17206	--	--	Functional
21/--	F	10/18/83	Pinguk R.	15	R8	R8	10032	10031	--	--	Functional
22/65	M	6/23/82	Pinguk R.	4	R65	R65	--	--	--	--	Animal dead, 12/19/85
23/--	M	4/13/84	Black Mt.	10+	R9	R9	--	17234	Red	Yel	Animal dead, 6/10/84
24/62	F	6/23/82	Nuluk R.	6	R62	R62	17201	17202	--	--	Functional
34/--	M	10/27/83	Don R.	12+	R11	R11	17211	17212	Blk	Yel	Last located, 10/02/84
35/--	F	3/21/86	Serp. Spngs.	4	R10	R10	16371	16370	--	--	Functional
37/--	F	10/18/83	Pinguk R.	5-6	R14	R14	--	--	Yel	Blk	Functional
39/--	F	4/12/84	Nuluk R.	10+	R15	R15	17238	17237	Red	--	Animal dead 07/17/85

Appendix A. Continued.

Animal/ visual collar number	Sex	Date collared	Location	Approximate age at collaring (years)	Plastic ear tag Nos. & color		Metal ear tag nos.		Horn streamer colors		Radio status, Jan 1987
					Left	Right	Left	Right	Left	Right	
41/--	M	4/12/84	Nuluk R.	4	R16	R16	17234	17233	Blk	Red	Functional
44/--	M	8/29/83	Solomon	2+	R1	R1	--	--	Red	Red	Last located 02/18/86
45/--	M	4/13/84	Black Mt.	7+	R17	R17	--	17240	--	--	Last located 5/03/84
46/--	M	3/21/86	Serp. Spngs.	3	R13	R13	16375	16374	--	--	Functional
48/--	M	6/06/84	Kougarok R.	8-9	R19	R19	--	17241	Yel	Yel	Animal dead; 11/01/84
50/--	M	8/05/85	Nome	7-8	--	--	--	--	--	--	Functional
1.16/--	M	4/22/86	Cp. Rodney	4	R38	R38	16365	16832	--	--	Functional
1.30/--	M	3/21/86	Serp. Spngs.	5	R45	R45	16373	16372	--	--	Functional
1.76/--	M	4/22/86	Cp. Rodney	4	R41	R41	16676	16367	--	--	Functional
1.90/--	M	3/21/86	Serp. Spngs.	3	--	--	16369	16368	--	--	Functional

[a] Not clear from transplant reports whether same tag number applied to both left and right ear tags.

Appendix B. Observed mortality of muskoxen on the Seward Peninsula, 1970-86.

Year	Sex and age	Location	Probable cause of death
1970	No mortalities reported	--	--
1971	Yearling female	On beach 50 km east of Nome	Fell through ice
	2 to 3-year-old female	Foothills between Sinuk & Feather Rivers	Bear kill?
1972	Adult, sex unknown	16 km below Tin City on beach	Drowned
1973	No mortalities reported	--	--
1974	6-year-old male	Near Selawik	Mistaken for bear & shot
1975	No mortalities reported	--	--
1976	No mortalities reported	--	--
1977	No mortalities reported	--	--
1978	No mortalities reported	--	--
1979	No mortalities reported	--	--
1980	No mortalities reported	--	--
1981	Radio-collared adult	3 km from Port Clarence	Fell through ice
	Yearling, sex unknown	Nuluk River	Unknown
	Adult male	Golden Gate Creek	Unknown
1982	2 adult females radio-collared in 1981	Tagagawik River	Unknown
	1 adult male	Near Teller	Illegal kill
1983	No mortalities reported	--	--

Appendix B. Continued.

Year	Sex and age	Location	Probable cause of death
1984	16-year-old male from 1970 transplant	Near Brevig	Unknown
	15-year-old radio-collared female from 1970 transplant, No. 12	Don R.	Unknown
	Adult female	Nuluk R.	Capture mort.
	3-year-old male	Nuluk R.	Capture mort.
	2 adult females	Pinguk R.	Capture mort.
	Adult female	Black Mt.	Capture mort.
	Radio-collared adult male, No. 48	N. of Teller	Unknown
1985	Adult male	Arctic R.	Unknown
	Radio-collared adult male, No. 14	Cooper Cr.	Unknown
1986	No mortalities reported		

Appendix C. Replicate measurements of selected blood parameters[a] of radio-collared muskoxen, Seward Peninsula, Alaska, April 1984.

No./sex	Date	Mg (mg/dl)	Ca (mg/dl)	HCT (%)	Hb (g/dl)	RBC (10^6/ l)	WBC (10^6/ l)	MCV (fl)	MCH	MCHC	PLTX10^3
14/M	04/12/84	2.7	10.4	41.3	15.9	8.53	4.8	49			
		2.9	10.7	42.3	15.8	8.50	4.8	50			
19/M	04/12/84	2.9	9.4	36.6	12.9	6.83	3.2	54			
		2.7	9.5	34.8	12.9	6.83	3.0	52			
41/M	04/12/84	2.8	9.5	48.7	13.0	7.40	4.4	67			
		2.7	9.6	35.5	13.3	7.04	3.0	51			
--/F	04/12/84	3.0	9.9	45.5	17.5	9.44	4.8	49			
		2.8	9.8	45.4	17.1	9.34	5.3	50			
35/F	04/12/84	2.7	9.5	41.6	15.9	7.94	6.6	53			
		2.6	9.6	43.1	15.4	8.22	6.3	53			
39/F	04/12/84	2.6	8.7	26.0	9.9	5.20	3.3	51			
		2.6	8.7	34.9	13.3	6.92	3.9	51			
45/M	04/13/84	2.7	10.6	47.3	14.0	7.97	3.5	60			
		2.6	11.0	37.8	14.1	7.74	4.6	50			
--/M	04/13/84	3.1	10.3	34.2	13.6	7.19	4.0	48			
		3.0	10.5	36.5	14.3	7.65	3.4	48			
--/F	04/13/84	2.9	9.5	39.9	15.1	8.01	3.9	50			
		2.9	9.5	40.8	15.0	8.11	4.2	51			

APPENDIX C. Continued.

No./sex	Date	Mg (mg/dl)	Ca (mg/dl)	HCT (%)	Hb (g/dl)	RBC (10^6/ l)	WBC (10^6/ l)	MCV (fl)	MCH	MCHC	PLTX10^3
1.30/M	03/21/86			40.8	17.4	7.62		53.6	22.9	42.7	1020
				40.8	17.4	7.62		53.6	22.9	42.7	1020
46/M	03/21/86			31.0	14.2	5.96		51.9	23.8	45.8	968
				31.0	14.2	5.96		51.9	23.8	45.8	968
				32.1	14.1	6.20		51.7	22.8	44.1	823
				32.1	14.1	6.20		51.7	22.8	44.1	823
1.76/M	04/22/86			29.2	12.3	5.39	14.6	54.1	22.8	42.1	768
48/M	06/06/84			36.8	13.9	7.20	3.7	52			
				36.8	13.8	7.21	3.5	52			
				36.5	14.0	7.21	3.4	51			
				36.5	14.1	7.25	3.5	51			

[a] Key to abbreviations used in table:

Mg-Magnesium
CA-Calcium
HCT-Hematocrit
HB-Hemoglobin
RBC-Red blood cells
WBC-White blood cells
MCV-Mixed cell volume
MCH-Mean corpuscular hemoglobin
MCHC-Mean corpuscular hemoglobin concentration
PLT-Platelets